CHAPTER XIII

THE EYES OF REPTILES

The portrait of GORDON L. WALLS (1905——) (Fig. 417) could suitably serve as an introduction to many chapters in this book for he has done much to correlate and rationalize our ideas on the structure and function of the eyes of Vertebrates. Originally trained as an engineer, he branched into zoology at Harvard University ; here, expecting to work on Rotifers, he was arbitrarily assigned a problem on the retina for investigation and for many years devoted all his energies to the study of the finer structure and function of this tissue throughout the vertebrate phylum. His most striking contribution in this field was his enthusiastic advocacy of the theory that the cones were more primitive than the rods and that in the evolutionary process the cones of an ancestral species transmuted into rods in a descendant species. It was in the eyes of Reptiles, particularly snakes, that he found the most satisfying evidence for his views, and his observations led him to formulate new ideas about the evolutionary history of groups such as these. His work in this field was summarized in his classical book, *The Vertebrate Eye and its Adaptive Radiation*, published in 1942, which is undoubtedly the most comprehensive and readable volume on this subject in the English literature ; to it I have been greatly indebted in the writing of this volume. This task completed, he forsook comparative ophthalmology and, as Professor of Physiological Optics at the University of California, he devoted his attention to the still more complex problems of colour vision and colour blindness, a subject wherein his contributions will be noted in a subsequent volume of this series.

Of the five main groups of extant Reptiles, the CHELONIANS (turtles, tortoises) are the most archaic and primitive ; the RHYNCHOCEPHALIANS (the sole extant representative of which is *Sphenodon*) have relatively simple eyes largely adapted for nocturnality ; the CROCODILIANS (crocodiles, alligators) again have relatively simple eyes largely adapted for vision under water ; the LACERTILIANS (lizards), active and (with many exceptions) typically diurnal creatures, have the most elaborately formed eyes among the entire class and the most typically reptilian in their characteristics; while OPHIDIANS (snakes) have eyes peculiar to themselves and in most of their essential features widely different from all other members of the group, bearing little resemblance to the eyes of their immediate ancestors, the lizards.

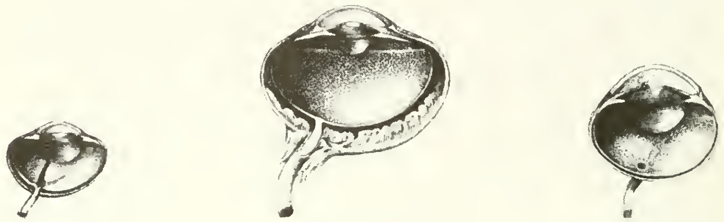
We shall therefore describe the eyes of lizards in some detail as the essential reptilian type, enumerate shortly the main simplifications seen in the first three groups, and finally discuss the unique eyes of snakes.

THE EYES OF REPTILES are the first to be finally and completely adapted to terrestrial life. We have already seen that those of the Ichthyopsida have many features in common and that although Amphibians, leaving the water after the larval stage, have acquired many adaptations for vision on dry land, their eyes still exhibit a

FIG. 417.—GORDON L. WALLS (1905——).

general plan broadly comparable with that of the eyes of Fishes. In the eyes of Sauropsida, however, a revolution has occurred. Even among the most primitive Reptiles adaptations of a different character and a much higher order are found, most of them having little apparent evolutionary relationship with the characteristics of the visual organs of surviving Amphibians, and these become perfected in their descendants, the Birds. The entire sauropsidan family will be found to have much in common, having evolved a type of eye very different from their ancestors and as different from the mammalian eye which has developed on entirely separate lines.

Fig. 418.—The Eyes of Reptiles.



The lizard, *Lacerta monitor.* — The tortoise, *Testudo mydas.* — The crocodile, *Crocodilus sclerops.*

Reproductions of Soemmerring's engravings (1818). The reproductions are life size and represent the lower half of a horizontal section of the left eye.

The essential features of the typical reptilian eye are the following (Fig. 418):

An effective accommodative mechanism depending on deformation of the lens—not its to-and-fro movement as in Ichthyopsida. This is effected by a striated ciliary muscle arising in the cornea and deriving firm leverage from a ring of scleral ossicles—a descendant of the tensor choroideæ of Fishes. To this is added a ventral transversalis muscle emerging from the region of the (closed) fœtal fissure, the function of which is to swing the lens nasally and attain the convergence necessary for binocular vision—homologous with the protractor lentis of Amphibians. The lens is necessarily soft and the subcapsular epithelial cells in the equatorial region have elongated enormously in a radial direction to form an annular pad to which are fused the ciliary processes, now tall and well-formed in contrast to the small ciliary folds hitherto found.

A striated iris musculature giving the iris considerable mobility.

An avascular retina nourished indirectly by the choroid and, in addition, through the conus papillaris (in lizards), or through a membrana vasculosa retinæ (in snakes).

A pattern of iris vascularization consisting of deep circumferential *arteries and superficial radial veins in place of the reverse arrangement in Ichthyopsida.*

An essentially simple retina with a cone population in diurnal species and a rod population in those with nocturnal habits ; each type of cell may be single or double and each may contain an oil-droplet.

THE LACERTILIAN EYE

Of LIZARDS there are some 20 families extant,[1] essentially inhabitants of the warmer regions of the earth ; they are active, agile animals, with an exoskeleton of scales often beautifully coloured, feeding usually on insects, worms and other small animals, although

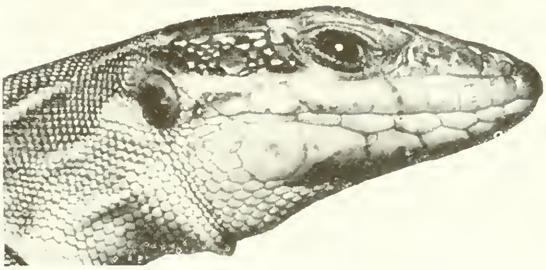


FIG. 419.—THE HEAD OF THE LIZARD, *Lacerta muralis* (× 3·5) (Katharine Tansley).

FIG. 420.—THE CHAMELEON (photograph by Michael Soley).

[1] Including the true lizards of the Old World deserts, the skinks, the geckos, the monitors (or dragons), iguanas, agamid lizards, Gila monsters, glass snakes, limbless slow-worms and the chameleon.

some (Iguanids) are vegetarian; they are mostly terrestrial, some arboreal, a few amphibious (the iguanid, *Amblyrhynchus cristatus* of the Galapagos Islands). Only exceptionally in sluggish limbless types are the eyes poorly developed—the Anguidæ (slow-worms) and the degenerate Amphisbænidæ of subterranean habits.

Chlamydosaurus

The EYEBALL is almost spherical although the antero-posterior axis is the shortest, but there is a marked concavity, the corneo-scleral sulcus, in the region of the junction of these two tissues (Fig. 421). The sclera is relatively thin and is supported over most of its extent by a scleral cartilage which, starting from the posterior pole, usually reaches to the equator or beyond (Fig. 422); occasionally, as in the chameleon,

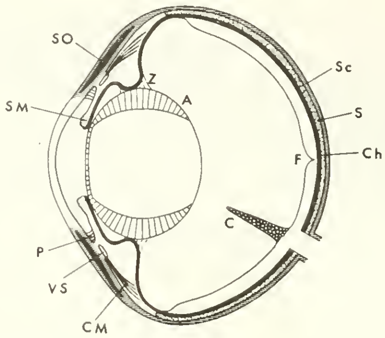


FIG. 421.—DIAGRAM OF THE EYE OF A LIZARD.

A, annular pad; C, conus; Ch, choroid; CM, ciliary muscle; F, fovea; P, pectinate ligament; S, scleral cartilage; Sc, sclera; SM, sphincter muscle; SO, scleral ossicles; VS, ciliary venous sinus; Z, zonule.

it is confined to a small disc in the foveal region. Anteriorly, and lying superficial to the cartilage when it is prolonged forwards, is a ring of some 14 scleral ossicles distributed around the deep corneo-scleral sulcus sometimes imbricated in 2 or 3 layers; these, noted by such early writers as Zinn (1754) and Soemmerring (1818), support and maintain the convexity of the globe in this region thus approximating the ciliary body to the lens. The *cornea* is circular and thin and has the usual layering characteristic of Vertebrates apart from the absence of Descemet's membrane and its endothelium in some geckos; its inner third merges with the pectinate ligament and gives rise to the ciliary muscle.

Gecko

The *uvea* in general is thin. The *choroid* forms a tenuous layer without distinctive characteristics. The *ciliary body* varies in shape—narrow and angular in the geckos, broad and rounded in the chameleon—and has no ciliary processes but abuts directly on the annular pad of the lens (Figs. 423–4). The musculature is complicated and is divided into 3 systems. The ciliary muscle (of Brücke) is well developed, the fibres running meridionally from their origin from the inner layers of the cornea, not to the choroid as does the tensor choroideæ of Fishes and Amphibians (or the ciliary muscle of Mammals), but to the orbiculus ciliaris, where its anchorage is continued by a TENACULAR LIGAMENT running from the orbiculus into the sclera. These fibres are particularly marked anteriorly, those arising from the cornea being to some extent isolated to form the MUSCLE OF CRAMPTON, a muscular bundle more fully developed in Birds.[1] The meridional ciliary fibres are sometimes augmented by circumferential fibres arising dorsally and extending round in the temporal half of the globe ; and in most species by an inferior TRANSVERSE MUSCLE. This muscle arises ventrally from the connective tissue between the ciliary body and the sclera and passes through an open portion of the fœtal cleft to be inserted into the zonular fibres and thus indirectly to the lens. It would seem analogous to the protractor lentis muscle of Amphibians and probably moves the lens nasally during accommodation, presumably to increase convergence (*Seps*, *Lacerta*—Leplat, 1921).

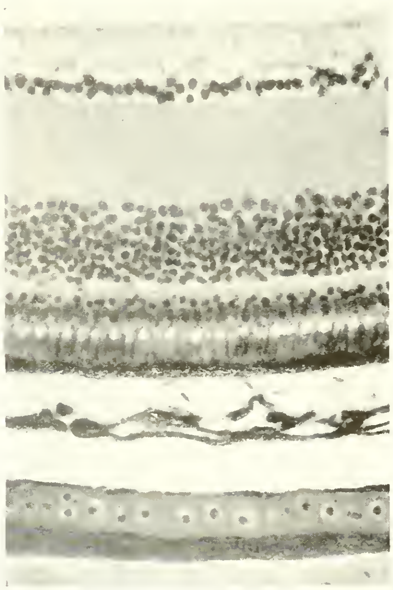


FIG. 422.—THE POSTERIOR SEGMENT OF THE EYE OF THE LIZARD.

Showing the retina, r, with its pigmentary epithelium, p, choroid, ch, scleral cartilage, s, and the fibrous sclera, sc (× 320) (Norman Ashton).

The *iris* is relatively thin at the periphery, but thick towards the pupillary margin where it forms a well-marked ramp. The two posterior ectodermal layers are deeply pigmented and from the anterior are derived the striated fibres of the pupillary musculature. The circumferential sphincter fibres are well developed. The dilatator fibres form a thin layer next the epithelium, their ordinarily radial direction assuming complex configurations in those species wherein the pupil is slit-shaped. The mesodermal portion of the iris is usually highly coloured as if in an attempt to make the eye conspicuous, sometimes with red, yellow and melanin pigments, sometimes, as in the chameleon, having a brilliant metallic sheen owing to a layer of guanine-

[1] p. 405.

Figs. 423 and 424.—The Ciliary Region of the Lacertilian Eye.

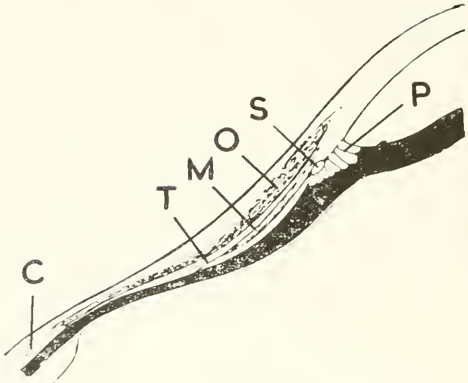


Fig. 423.—The lizard, *Tupinambis*.

C, scleral cartilage ; *M*, ciliary muscle ; *O*, scleral ossicles ; *P*, pectinate ligament ; *S*, ciliary venous sinus ; *T*, tenacular ligament (after Franz).

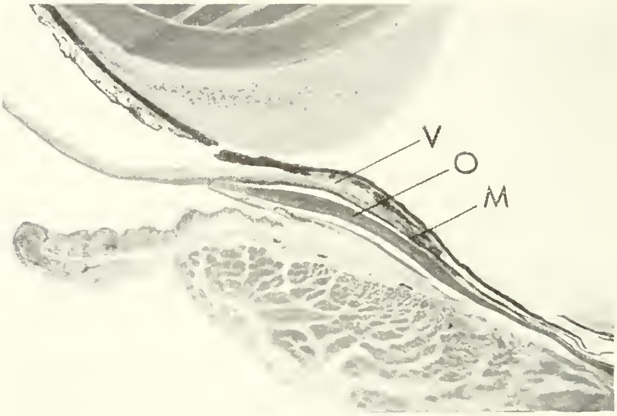


Fig. 424.—The skink.

M, ciliary muscle ; *O*, scleral ossicles ; *V*, ciliary venous sinus (× 60) (Norman Ashton).

containing iridocytes (Plate V).[1] The vascular arrangements resemble those of the salamander ; the two feeding arteries enter peripherally below and to the temporal side and run circumferentially but, in contradistinction to the arrangement in amphibian eyes, the veins lie superficially forming a plexus of radial vessels which are usually conspicuous ; the capillary zone is of varying width but is often con-

Iguana tuberculata

[1] The irides of many lizards compare in their remarkable brilliance with those of the parrots. In the green lizard, *Lacerta viridis*, they are of brightly speckled gold ; in *Iguana tuberculata* they show an exceedingly delicate festooned pattern of gold and [illegible] fibres ; in the geckos, a striped pattern of dark brown in a light yellow-ochre, [illegible] or grey background ; and so on.

PLATE V

THE IRIDES OF LIZARDS
(Ida Mann)

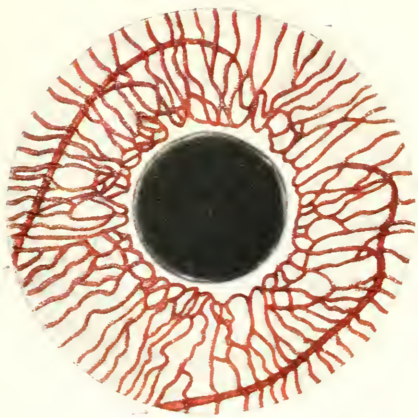


FIG. 1.—Cochin-China water-lizard, *Physignathus cochinchinensis* (right eye).

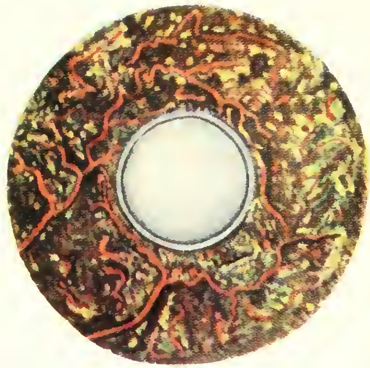


FIG. 2.—Agamid lizard, *Agama agama.*

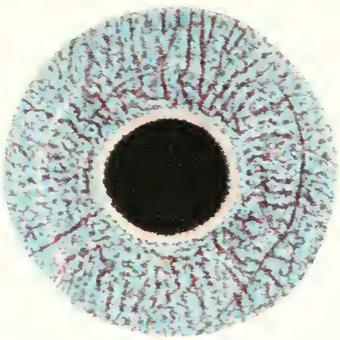


FIG. 3.—Yrpha iguana, *Ophryoessa superciliosa.*

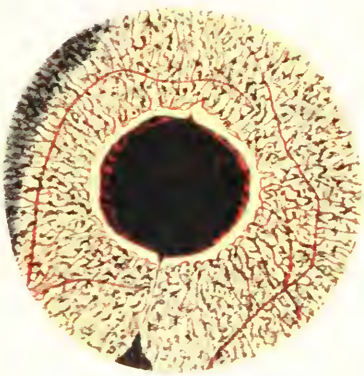


FIG. 4.—African plated lizard, *Gerrhosaurus grandis.*

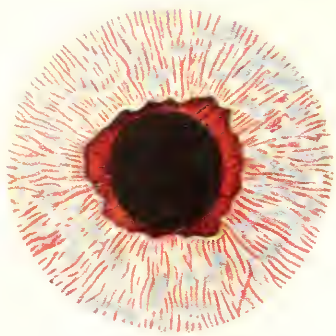
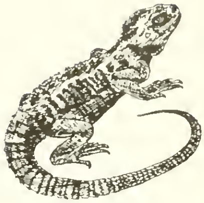


FIG. 5.—Black-pointed teju, *Tupinambis nigropunctatus.*

[*To face p.* 358.

fined to the thickened rim of the pupillary margin (Mann, 1929). This vascular pattern may to some extent be obscured by the pigment of the multicoloured iris (*Agama*) but stands out in prominent relief in those irides provided with a guanine layer on which, indeed, the vessels may cast shadows; it is to be noted that the general arrangement of deep circumferential arteries and superficial radial veins, found commonly among Sauropsida, is completely different from the ichthyopsidan plan.



Agama

The angle of the anterior chamber is occupied by a loose pectinate ligament bridging over the space between the cornea and the anterior

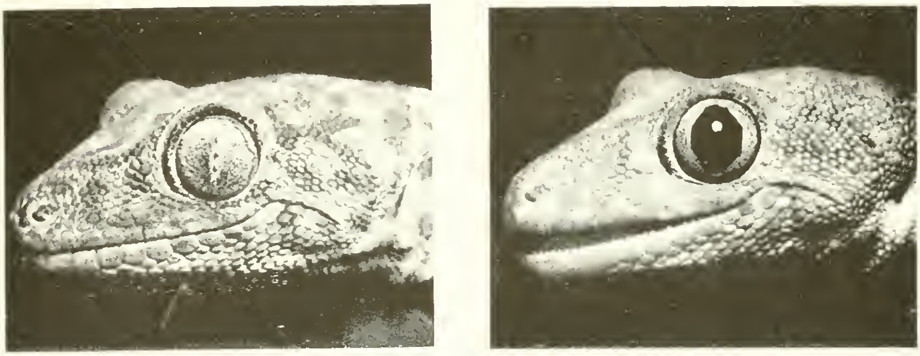


FIG. 425.—THE PUPILS OF A NOCTURNAL GECKO.

The Tokay gecko, so called from its chirping cry "Tuk-kaa." On the left, the pupil contracted by bright light, showing its reduction to a slit with three stenopœic openings. On the right, the wide hexagonal pupil in darkness photographed by infra-red light. (New York Zoological Society; photographs by Sam Dunton; from the *Illustrated London News*.)

chamber, while a ciliary sinus,[1] venous in nature but usually devoid of blood, runs circumferentially around the region of the angle separated from the sclera by fibres of the ciliary muscle (Lauber, 1931) (Figs. 423–4).

The *pupil* in diurnal lizards is usually round and relatively immobile, in nocturnal lizards extremely active and contracting to a slit-shape (with the exception of the Gila monster, *Heloderma*, which has circular pupils, Walls, 1934). Of the latter type, a typical slit-shaped pupil is seen in the Mexican night lizard, *Xantusia* (Kahmann, 1932–33). In this class, however, the most interesting is the pupil of the nocturnal geckos (Fig. 425) which is somewhat reminiscent of that seen in the dogfish, *Scylliorhinus* (Fig. 313) and in some rays, (Fig. 312). The diurnal geckos, like the great majority of lizards, have a round pupil, remaining circular on contraction and little if at all affected by sunlight or drugs, but in the nocturnal types in diffuse

Heloderma

[1] Analogous to the canal of Schlemm.

FIGS. 426 TO 428.—THE LENSES OF LIZARDS.

FIG. 426.—Section through the annular pad of the skink. The iris and cornea above and to the right (× 70) (Norman Ashton).

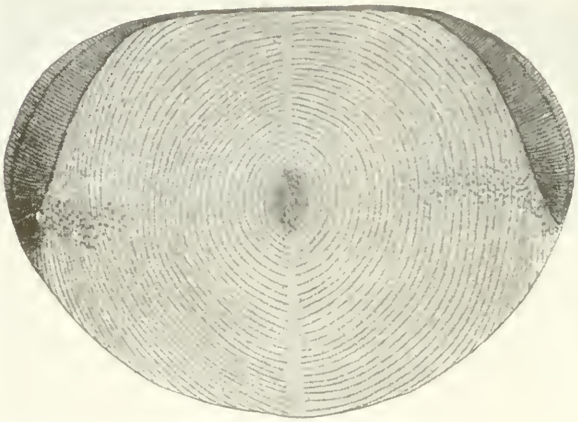


FIG. 427.—The lens of *Lacerta*, showing a small annular pad (after Rabl).

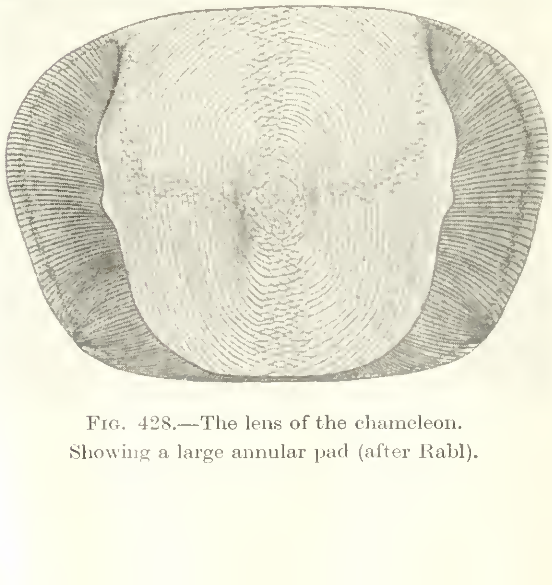


FIG. 428.—The lens of the chameleon.
Showing a large annular pad (after Rabl).

light the pupil assumes the form of a vertical slit with several paired notches on its margins ; on contraction in bright light the slit completely closes leaving only a row of stenopœic openings down its length, which, acting together, would produce an image of considerable clarity without any dioptric mechanism or accommodative adjustment (Fig. 425) (Beer, 1898 ; Läsker, 1934). Such an arrangement is undoubtedly of considerable visual value, and Johnson (1927) after repeated observation concluded that to some extent the movements of this exceedingly sensitive pupil were under voluntary control.[1]

The *lens* is typically sauropsidan (Beer, 1898 ; Rabl, 1898). In size it is voluminous, particularly in nocturnal types ; in shape it is flattened antero-posteriorly with a low curvature on its anterior surface and a high convexity posteriorly except in nocturnal types, particularly the gecko, wherein it is almost spherical ; in consistency it is soft and readily mouldable with a thin capsule : and, as in Cyclostomes, sutures are usually absent for the fibres terminate in one circumscribed area anteriorly and posteriorly. The most characteristic feature, however, is the equatorial ANNULAR PAD,[2] formed by the radial growth of the subcapsular epithelium in this region which elongates to such an extent that it abuts against the ciliary body. In most lizards the pad is marked, in the chameleon enormous, the thickest known among Sauropsida (Figs. 426–8). The zonular fibres arising from a broad area of the ciliary body are attached to this structure. In one diurnal gecko (*Lygodactylus*) the lens is coloured with a yellow pigment.

The *retina* of lizards shows many interesting peculiarities.[3] The pigment epithelium is well formed with numerous long, fine processes dipping down permanently between the outer segments of the visual cells. The extent of the migration of pigment with variations of light is small (3μ in *Sceloporus*) ; and the contraction of the cones on exposure to light is also minimal (Detwiler, 1916–23).


Anolis

As seen ophthalmoscopically, the fundus of lizards varies in its appearance in the different genera, but it shows the same general characteristics (Plate VI, Figs. 1 to 5). The background tends to be uniform—usually slate-grey (as in the alligator lizard, *Anolis alligator*), sometimes dark or almost black (as in *Lacerta galloti*), brick-red in the nocturnal geckos (grey in diurnal types), and exceptionally green (as in the iguanid, *Conolophus cristatus*) or variegated (as grey in the upper half and dark red below in the iguanid, *Metopoceros cornutus*). Sometimes it is heavily besprinkled with white spots (*Lacerta galloti*),

[1] Compare the pupils of seals and sea-lions, p. 470.

[2] An annular pad situated laterally is marked in Chelonians, Crocodilians and lizards (thin in geckos and snake-lizards). It is vestigial in Monotremes and some Marsupials. It is situated anteriorly in Ophidians.

[3] Krause (1863–93), Schultze (1866–67), Ranvier (1889), Hess (1912), Franz (1913), Rochon-Duvigneaud (1917–43), Verrier (1930–32), Kahmann (1933), Walls (1934–42), Underwood (1951).

while in *Conolophus cristatus* there are yellow spots over the green background. Usually the semi-opaque nerve fibres radiate uniformly outwards from the disc, sometimes, as in the American "glass-snake," *Ophisaurus ventralis*, coarse in texture, sometimes so fine as to be barely visible (the leaf-footed lizard, *Pygopus lepidopus*, *Chamæleon*). The disc itself is circular and white but is practically entirely obscured by the conus. The retina is invariably entirely avascular.

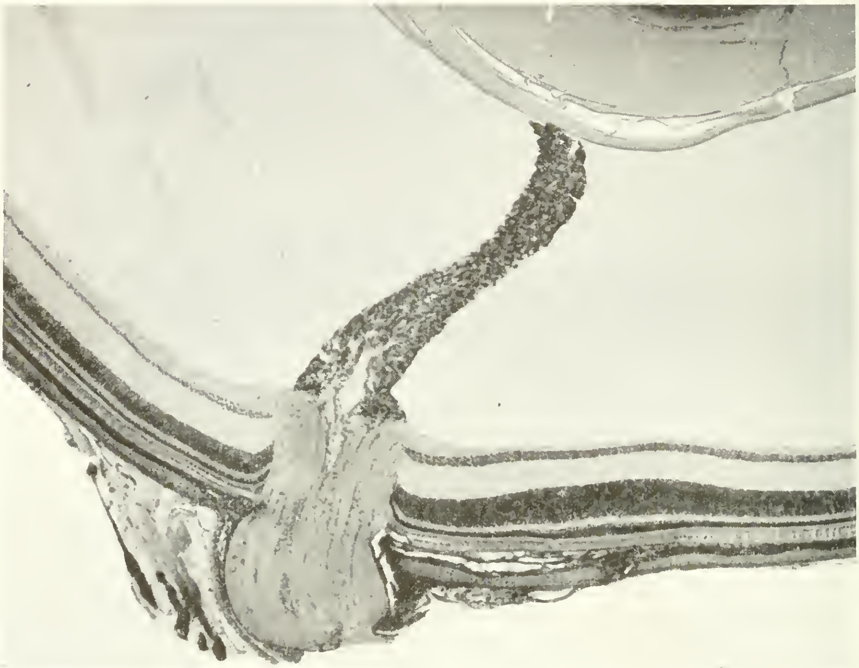


FIG. 429.—THE POSTERIOR POLE OF THE EYE OF THE LIZARD, *LACERTA MURALIS*. Showing the optic nerve and the conus papillaris approaching the lens (× 50) (Katharine Tansley).

Nutrition is conveyed to the retina by a peculiar vascular structure, the CONUS PAPILLARIS, an outgrowth of glial tissue from the optic disc supplied by an artery and vein issuing from the optic nerve and derived from the hyaloid (not the choroidal) vascular system (Fig. 429). Originally described by Soemmerring (1818) in the eye of lizards (*Lacerta monitor*, *L. vulgaris*, *L. iguana*), the conus has attracted a great deal of study.[1] It is a richly vascular structure with a central artery and vein surrounded by a thick layer of wide capillaries heavily dusted with pigment granules, the whole lying in a framework of neuroglial tissue

[1] [illegible] (1853), Hulke (1864), H. Müller (1862), Beauregard (1876), Kopsch (1892), [illegible]w (1901), Jokl (1923), Johnson (1927), and many others.

PLATE VI

The Fundi of Lizards

(Lindsay Johnson)

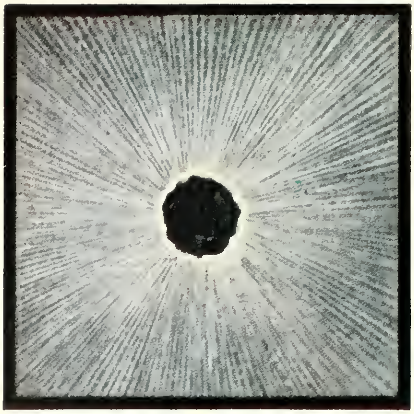


Fig. 1.—Alligator lizard, *Anolis alligator.*

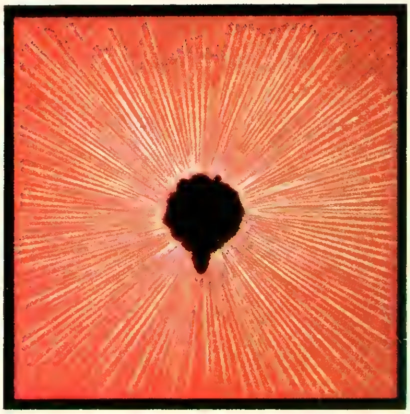


Fig. 2.—Turkish gecko, *Hemidactylus turcious.*

Fig. 3.—Galopagoan iguanid, *Conolophus subcristatus.*

Fig. 4.—Black ig[illegible] *Metopoceros cornutus.*

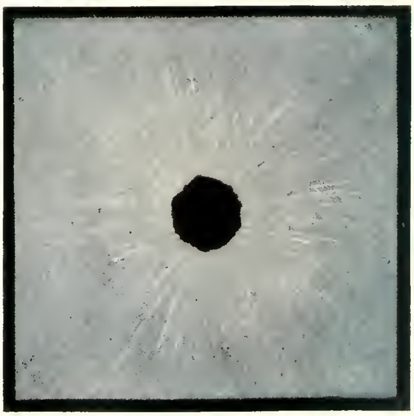


Fig. 5.—Chameleon, *Chamæleon vulgaris.*

(Franz, 1913 ; Jokl, 1923). Considerable variations occur in size and shape. As a rule it is a relatively simple structure and only in some Iguanids (particularly *Conolophus* and *Metopoceros*, Plate VI) does it become plicated and approach the complexity and beauty of the pecten of Birds. It may be circular in cross-section, oval, X- or Y-shaped (as in the monitor lizard, *Varanus*) ; it may be short and stumpy, forming a small cushion-like papilla on the disc, as in nocturnal

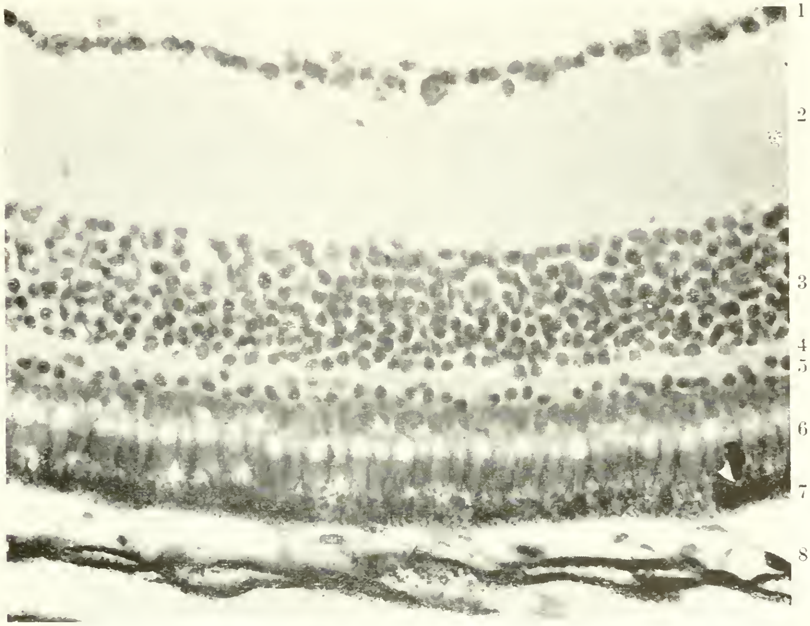


FIG. 430.—THE RETINA OF THE LIZARD.

(1) ganglion cells ; (2) inner plexiform layer ; (3) inner nuclear layer ; (4) outer plexiform layer ; (5) outer nuclear layer ; (6) visual cells ; (7) pigmentary epithelium ; (8) choroid (× 500) (Norman Ashton).

forms (most geckos: the leaf-footed lizard, *Pygopus*) or in the chameleon, or long and slender pointing towards the centre of the globe (the slow-worm, *Anguis fragilis*), sometimes nearly reaching the lens (the green lizard of Southern Europe, *Lacerta viridis*) ; only in the degenerate burrowing types (Amphisbænidæ, etc.) is the conus lacking.[1]

Anguis

In its histological structure the retina itself is avascular, thick and richly cellular with a well-defined lamination (Fig. 430) ; the inner nuclear layer with 9 or 10 rows of superimposed nuclei is compact and the ganglion cell layer with 2 or 3 rows of cells is particularly well-developed and conspicuous. The visual cells in most species are of two

[1] p. 733.

types, showing a variation in configuration from typical cones to rods (Walls, 1934) (Figs. 431–3). In the great majority of lizards of diurnal habit there are typical single and double cones ; the single cones have a yellow oil-droplet ; of the double cones, one element has an oil-droplet and the other a voluminous paraboloid (Krause, 1863). In some geckos, Underwood (1951) described another type of double visual cell wherein each member possessed a paraboloid and an ellipsoid while the

FIGS. 431 TO 433.—VISUAL CELLS OF LIZARDS.

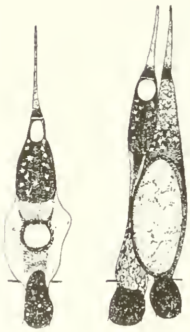


FIG. 431.—The cones of a diurnal lizard, *Crotaphytus*.

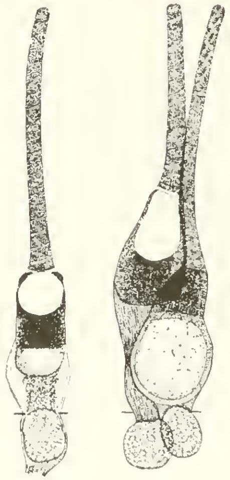


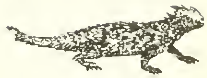
FIG. 432.—The cones of a nocturnal lizard, *Xantusia*.

FIG. 433.—The rods of a gecko, *Coleonyx* (× 1,000) (Gordon Walls).

larger member had an oil-droplet.[1] In some nocturnal species the droplets are discarded (the worm-lizard, *Aniella* ; the poisonous Gila monster of Mexico and Arizona, *Heloderma*) or colourless (the night lizard, *Xantusia*, Heinemann, 1877), but the outer segments of the visual cells, both single and double, are elongated and rod-like although rhodopsin is lacking. In the nocturnal geckos, however, both elements are frankly slim and rod-like and the long outer segments contain an abundance of visual purple ; these should therefore be considered as rods (Detwiler, 1923 ; Walls, 1942). There is little convergence in the retina; Vilter (1949), indeed, found that the ratio between visual cells and ganglion cells was approximately unity.

[1] In *Aristelliger* Underwood noted occasional triple visual cells.

The eyes of diurnal lizards contain a central area at the posterior pole wherein the cones are longer and thinner than in the peripheral retina ; in addition, in diurnal varieties a central fovea is present wherein the cones are closely packed, long and filamentous (Fig. 434). The fovea is very striking in such forms as the American horned "toad," *Phrynosoma* (Detwiler and Laurens, 1920 ; Ochoterena, 1949), but is seen in its most fully developed form in the chameleon. The



Phrynosoma

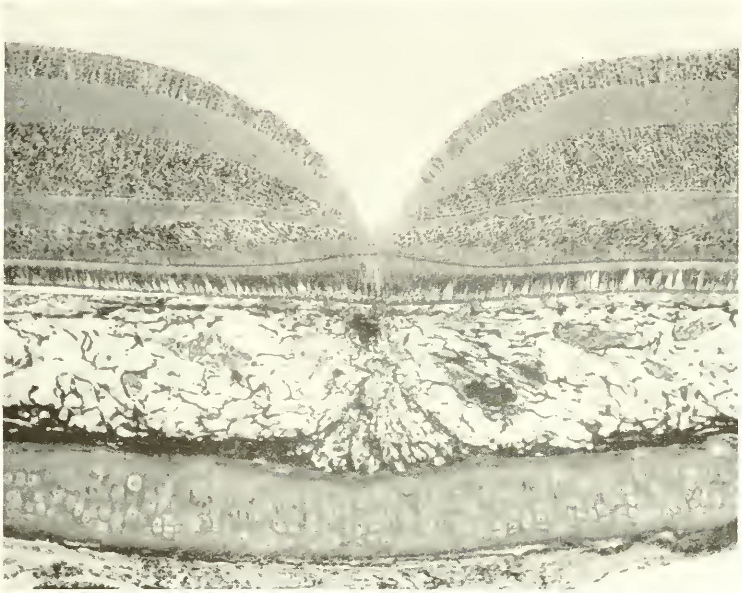


FIG. 434.—THE REMARKABLY WELL-FORMED FOVEA OF THE GIPPSLAND WATER-DRAGON, *PHYSIGNATHUS* (O'Day).

ch, the thick choroid ; *r*, the remarkably well-formed retina ; *s*, scleral cartilage ; *sc*, sclera ; *v*, visual cells.

remarkable fovea of this animal wherein the cones are longer (100μ), their concentration higher (756,000/sq. mm.), and the pit deeper than in the fovea of man, has long excited admiration (H. Müller, 1861–72 ; Chievitz, 1889 ; Walls, 1942 ; Detwiler, 1943 ; Rochon-Duvigneaud, 1943 ; and others). In nocturnal species, on the other hand, only a trace of a foveal pit may be observed (*Xantusia*) or it may be entirely lacking (*Heloderma*, and usually in the geckos). In some geckos a shallow temporal fovea exists (*Gonatodes fuscus*, *Sphærodactylus argus*, *S. parkeri*, Underwood, 1951)[1] ; while in certain arboreally active species of the diurnal lizard, *Anolis*, in addition to the deep central fovea, a

[1] *Gonatodes* has a pure-cone retina, *Sphærodactylus argus* has visual elements intermediate between rods and cones, *S. parkeri* has a pure-rod retina and, incidentally, a pure-rod fovea.

shallow temporal one may also be present containing both single and double cones (Underwood, 1951) ; this is the only known occurrence of a bifoveate retina apart from Birds. It is to be noted that with their lateral eyes and small binocular field (about 20°, Kahmann, 1932) binocular fixation with the central foveæ of lizards is out of the question; each is used monocularly and independently except, perhaps, for the chameleon with its quite extraordinary ocular movements.[1] The shallow temporal fovea in *Anolis* can, however, be used for binocular vision to assist in its agile arboreal activities.

The *optic nerve* does not have a well-defined and orderly fascicular system and throughout it the oligodendroglial cells are somewhat irregularly scattered (Prince, 1955).

Chameleon

THE OCULAR ADNEXA. Most lizards possess two *eyelids* outlining a horizontal palpebral aperture (Fig. 419), and with the exception of an iguanid, *Anolis alligator*, a species of American " chameleon " in which the two lids move equally, the upper lid is more or less stationary, the lower mobile as is usual in the lower Vertebrates ; the latter is often supported by a tarsal plate of fibrous tissue and moved by a retractor muscle attached to its lower border and arising from the depths of the orbit (Cords, 1922 ; Anelli, 1936).[2] In some forms (*Chamæleon*) in which the globe is very large, the palpebral aperture is constricted to the size of the pupil and the lids move with the eyeball (Figs. 420 and 845). In this lizard the lids are exceedingly soft and thin and rarely close ; when they do they form a horizontal slit at the same time pushing the eye backwards into the orbit.

Skink

In a number of lizards belonging to the families Lacertidæ (as *Eremias*, *Cabrita* and *Ophiops*), Tejidæ and Scincidæ, and in some species as *Cordylosaurus*, *Lanthanotus* and some West Indian members of the iguanid genus, *Anolis*, there is a transparent window in the lower lid where the scales are reduced or absent through which vision is possible when the lid is drawn upwards ; alternatively, as in the Iguanids, two or three black-bordered scales are semi-transparent, forming, as it were, a window with panes of glass through which some vision is possible (Figs. 435–441). The area involved is small and when the eye is opened the window is concealed in a fold in the lower lid. Most of these lizards live in deserts or a rocky habitat and it is probable that such a window may serve as a protective measure against abrasion by sand or grit (Walls, 1934). In other cases (as the West Indian Anolinæ) the animals inhabit dark caves and frequently come out to the sun ; it may be that the black-bordered scales act as dark glasses as a protection against the sun in an animal with a relatively immobile pupil (Plate, 1924 ; Mertens, 1954 ; Williams and Hecht, 1955). In others again, particularly burrowing lizards, the skink, *Ablepharus*, and those which like the geckos crawl in gravel and stubble, as a protective measure the transparent lower lid is fused with the upper to constitute a " secondary spectacle "[3] fitting over the globe

[1] p. 694.
[2] Only in some Mammals (the leopard, bat and hedgehog) is cartilage found in ...rsal plate.
p. 266.

like a contact glass and separated from it by a closed conjunctival sac as is seen in snakes (Schwarz-Karsten, 1933 ; Walls, 1934 ; Verrier, 1936 ; Rochon-Duvigneaud, 1943). In such cases the spectacle may be surrounded by a rim of tiny scales, as in *Ablepharus*, *Ophiops*, or the geckos (Fig. 435) ; alternatively, as in snakes, such a rim-formation is lacking and the spectacle is inserted into the ordinary arrangement of the scales of the head (Fig. 436). It is

FIGS. 435 TO 441.—THE EYELIDS OF LIZARDS.

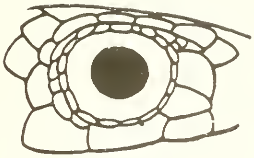


FIG. 435.—*Ablepharus*.

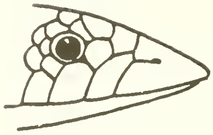


FIG. 436.—*Typhlœontias*.

There is a secondary spectacle formed by the fused transparent lids. In *Ablepharus* this is surrounded by a ring of scales ; in *Typhlœontias* this is absent.

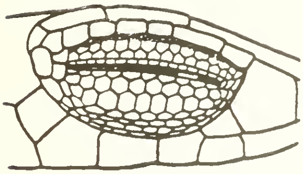


FIG. 437.—*Zonosaurus*.

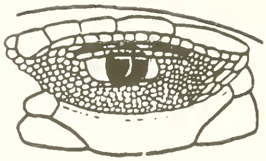


FIG. 438.—*Eremias*.

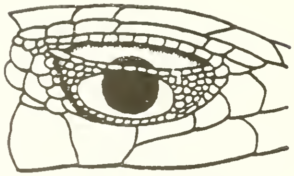


FIG. 439.—*Mabuya*.

The lower lid is mobile. In *Zonosaurus* the scaly lower lid rises to meet the upper lid ; in *Eremias* the central scales are transparent ; in *Mabuya* the central scales are lacking (after Angel).

FIG. 440.—*Anolis lucius*.

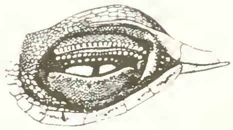


FIG. 441.—*Anolis argenteolus*.

The mobile lower lid has semi-transparent scales (3 in *A. lucius*, 2 in *A. argenteolus*) with a black bordered edge (Williams and Hecht).

exceptional for eyelids to be absent, as in *Pachydactylus maculatus*, one of the geckos wherein they are represented only by a thickened dermal fringe around the periphery of the eye.

When the lower lid is mobile and opaque, a transparent nictitating membrane is formed from a vertical fold of the conjunctiva at the nasal corner of the palpebral aperture which can be swept across the cornea from the nasal to the temporal side. Moisture and lubrication are usually attained by a lacrimal gland with several contractile ducts at the temporal canthus and a large harderian gland lying naso-ventrally provided with a single duct (Loewenthal, 1935–36 ; Schwarz-Karsten, 1937 ; Bellairs and Boyd, 1947–50). The lacrimal gland, however, is absent in the chameleon and many geckos. The naso-lacrimal duct enters the nose within the accessory olfactory vomero-nasal organ of Jacobson. The nictitating membrane is pulled across by a tendon-like cord arising from its free edge and attached to the dorsal wall of the orbit, its movements being controlled by a special arrangement of muscles behind the eyeball (Fig. 442).

In addition to the rectus muscles and a well-formed retractor bulbi, two extra muscles are inserted into the posterior aspect of the globe, both supplied by the VIth cranial nerve (Fig. 443). The first, the BURSALIS (QUADRATUS) MUSCLE, is inserted into the sclera near the

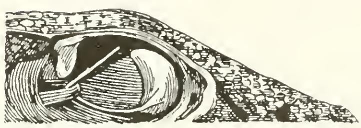


FIG. 442.—THE ORBIT OF THE MONITOR, *VARANUS*.

With the eye removed showing the nictitating membrane with its tendon looping through the bursalis muscle (after Bland-Sutton).

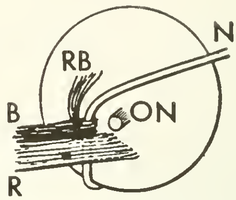


FIG. 443.—THE POSTERIOR ASPECT OF THE GLOBE OF *LACERTA*.

B, bursalis muscle ; N, the tendon of the nictitans ; ON, optic nerve ; R, retractor bulbi muscle ; RB, retractor bursalis muscle (after Franz).

optic nerve and round it the tendon of the nictitating membrane loops so that the latter is drawn taut when the muscle contracts ; from it a muscular slip runs upwards to be inserted more dorsally in the sclera, the RETRACTOR BURSALIS, which acts by bracing the bursalis so that the muscular apparatus and the looped tendon are kept away from the optic nerve when contraction occurs. In most lizards ocular movements are sluggish or occasionally absent, a marked and extraordinary exception being the insectivorous chameleon [1] : in it the extra-ocular muscles are very fully developed (Leblanc, 1925).

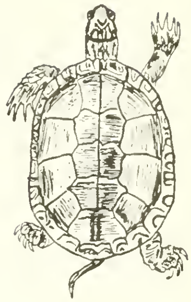
The *orbit* of lizards is open and fenestrated, a peculiarity being that the optic nerves pass through several openings in the endocranium ; the posterior bony wall is very deficient to allow room for a wide gape of the jaws.

THE CHELONIAN EYE

THE TORTOISES AND TURTLES are the most ancient of surviving Reptiles [2]—sluggish animals encased in a dorsal and ventral bony carapace into the shelter of which the head as well as the limbs and tail can

[1] p. 694. [2] p. 234.

be withdrawn. The Chelonia are divided into two sub-groups—of the first, wherein the vertebræ and ribs are free from the carapace, *Dermochelys coriacea*, a huge marine turtle sometimes 6 feet in length, widely but sparsely distributed in tropical seas, is the sole representative. The second group, with dorsal vertebræ and ribs fused in the carapace, comprises the CHELONIDÆ, marine and amphibious turtles with paddle-like flippers living on or near the shores of tropical seas, and the TESTUDINIDÆ, land tortoises with feet provided with toes adapted for walking, found widely in the warmer regions of the Eastern and Western Hemispheres (Fig. 444); among these the terrapins form an intermediate group with webbed toes.



Turtle

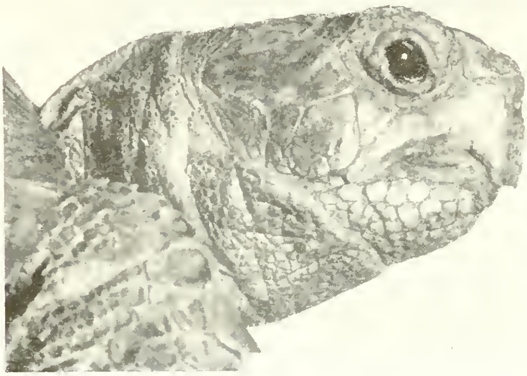


FIG. 444.—THE HEAD OF THE TORTOISE, *TESTUDO* (Katharine Tansley).

The eyes of the Chelonians, described and beautifully figured by Albers (1808) and Soemmerring (1818), and intensively studied by Kopsch (1892), bear a close resemblance to the lacertilian eye just described, but in general are more simple in structure; there are, however, some major differences—*the presence of ciliary processes, the participation of the sphincter pupillæ in the act of accommodation, and the absence of a conus* (Figs. 445 and 446).

The GLOBE is comparatively small and the cornea, instead of projecting forwards, continues the curvature of the sclera so that the corneo-scleral sulcus is insignificant. The epithelium is thick, Bowman's membrane absent and the endothelium markedly developed (Fig. 448). The scleral ossicles are imbricated in several layers so that the edge of one lamella is inserted between two others. Their numbers vary from 6 to 15,[1] while the scleral cartilage is very thick (1 cm. in the

[1] The scleral ossicles number 6–9 in the Greek tortoise, *Testudo græca*; 10 in the tortoise, *Emys* (König, 1934); 15 in the Mauritius tortoise (Rochon-Duvigneaud, 1943); and so on.

FIGS. 445 AND 446.—THE CHELONIAN EYE.

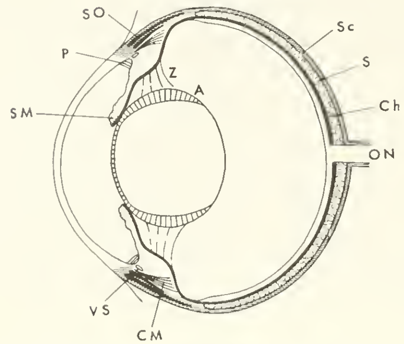


FIG. 445.—Diagram of a Chelonian eye.

A, annular pad ; Ch, choroid ; CM, ciliary muscle ; ON, optic nerve ; P, pectinate ligament ; S, scleral cartilage ; Sc, sclera ; SM, sphincter muscle ; SO, scleral ossicles ; VS, ciliary venous sinus ; Z, zonule.

FIG. 446.—Section through the eye of the tortoise, *Testudo* (Norman Ashton).

leathery-skinned turtle, *Dermochelys*, Rochon-Duvigneaud, 1943) (Fig. 447). In aquatic forms, the iris has the same bright and variegated colour as in the lizard—red, yellow, green and brown—and in some types is striped in such a way that the pattern on the skin is continued over the iris as if for the purposes of camouflage (the terrapin, *Clem*[illegible] Mann, 1931 ; and particularly the painted turtle, *Chrysemys*, Walls, 1942) (Plate VII).[1] In the land tortoises the colours are less bright, brown predominating. The common box tortoise, *Testudo carolina*, is peculiar in that it shows a remarkable instance of sexual dimorphism, the iris of the male being red, of the female brown.

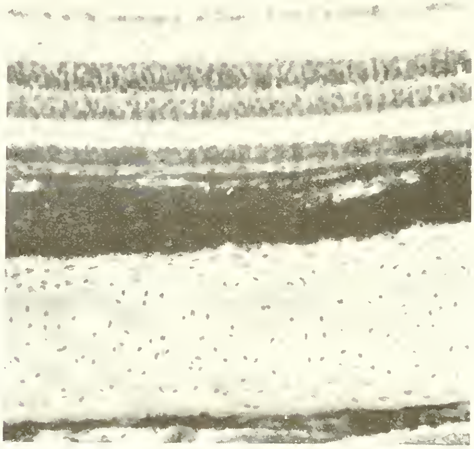


Fig. 447.—The Posterior Segment of the Eye of the Tortoise.
1, the retina ; 2, choroid ; 3, scleral cartilage ; 4. fibrous sclera (× 112) (Katharine Tansley).

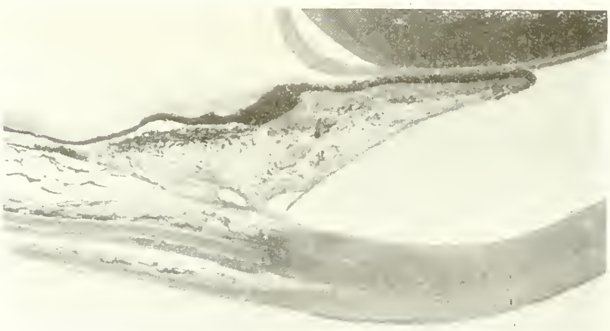
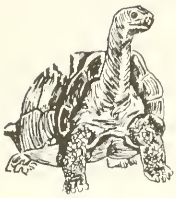


Fig. 448.—The Ciliary Region of the Eye of the Tortoise.

Note the immensely thick corneal epithelium, the scleral ossicles, *O*, arranged in layers, the trabecular tissue forming a pectinate ligament across the angle of the anterior chamber, and the highly developed sphincter of the pupil. The vessel lying internal to the angle of the anterior chamber is the ciliary venous sinus, homologue of the canal of Schlemm (× 60) (Norman Ashton).

[1] This matching of the colour of the iris to form an "eye mask" in a uniform pattern with the colours of the head is also well seen in such fish as the lidless lion-fish, *Pterois* ; in Amphibians, such as the frog, *Rana sphenocephala*, the newt, *Triturus torosus* : in Reptiles, such as the tree-snake, *Oxybelis* (See Cott, 1940 ; O'Day, 1942).

The *pupil* is circular and immobile both to light and drugs although its sphincter is powerful ; this muscle is essentially accommodative in function (Fritzberg, 1912). The ciliary body separates abruptly from the sclera to approach the lens leaving the angle of the anterior chamber deep and cleft-like ; the angle is traversed by the loose pectinate ligament linking the iris with the cornea, while deep in the cleft lies the ciliary venous sinus. The ciliary body has some 60 well-marked ciliary processes which abut against the lens in accommodation. The striated musculature resembles that of the lacertilian eye with the ventral transversalis muscle usually well-developed (Brücke, 1846 ; Mercanti, 1883 ; Hess, 1912 ; Fritzberg, 1912) ; the latter is absent in some forms (*Testudo*, König, 1934). The vascular arrangements of the uveal tract are of the usual reptilian type (Fritzberg, 1912).



Tortoise

The *lens* is extremely soft and almost fluid in consistency, probably the most readily moulded in the vertebrate phylum, and while it takes the form of a flat ellipse in land tortoises, it is of necessity almost spherical in sea turtles ; the annular pad is small.

The *fundus oculi* of Chelonians as seen ophthalmoscopically is singularly primitive and uniform (Plate VII, Fig. 3). The background is orange-red and from the circular disc readily visible nerve fibres radiate to the periphery, sometimes, as in the snapping turtle, *Chelydra serpentina*, almost completely obscuring the background. The disc is without a conus and is white, apart from a brownish patch of pigment in the Murray turtle, *Chelodina longicollis*, in which the nerve fibres are few and faintly marked.

The fundus of the Burgoma soft-shelled turtle, *Emyda granosa*, is unique (Plate VII, Fig. 4). The background is of brownish pink with red dots, and the large white disc is surrounded by a red choroidal ring outside which the nerve fibres radiate giving the appearance of a solar corona (Johnson, 1927).

Histologically the retina does not reach the high degree of definition in its architecture found in the lizard ; throughout its extent the different layers are by no means exclusively segregated but their elements tend to be intermingled (Figs. 449–452).[1] In the early stages of development an avascular glial cone may appear on the optic disc in some turtles [2] but this always disappears in the adult ; the retina is thus entirely avascular depending only on the choroid for its nourishment. The visual cells show a vast predominance of cones, either single or double, the former and one element of the latter containing an oil-droplet, orange, yellow or ruby-red in colour. Cells with a cone-like structure but resembling rods in the heaviness of the outer segment

[1] See Hulke (1864), Heinemann (1877), Chievitz (1889), W. Krause (1893), Pütter (1912).

[2] In the sea-turtle, *Chelonia*, the snapping turtle, *Chelydra*, the painted turtle, *Chrysemys*, etc.

PLATE VII

THE EYES OF CHELONIANS

FIG. 1.—The iris of the painted turtle. *Chrysemys picta* (Ida Mann).

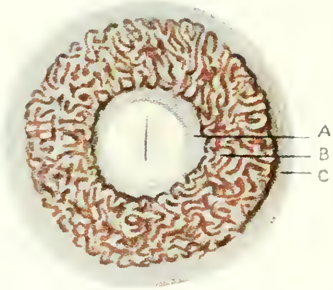


FIG. 2.—The iris of the European pond-tortoise, *Emys orbicularis*. *A*, thin circumpupillary zone; *B*, capillary plexus; *C*, zone of large vessels hidden by pigment (Ida Mann).

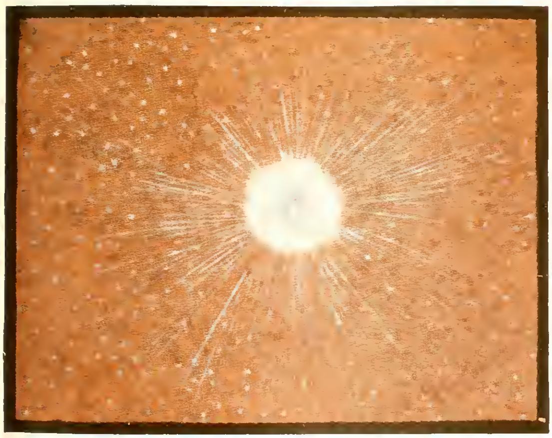


FIG. 3.—The fundus of *Cinyxis erosa* (Lindsay Johnson).

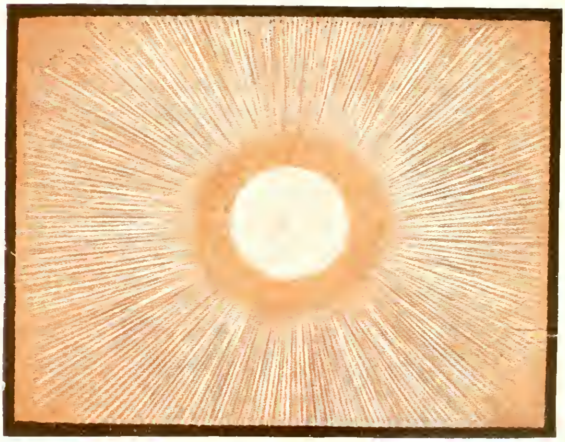


FIG. 4.—The fundus of the Burgoma river turtle, *Emyda granosa* (Lindsay Johnson).

FIGS. 449 TO 451.—THE CHELONIAN RETINA.

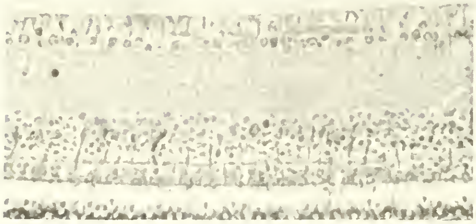


FIG. 449.—The retina of the tortoise (× 200) (Norman Ashton).

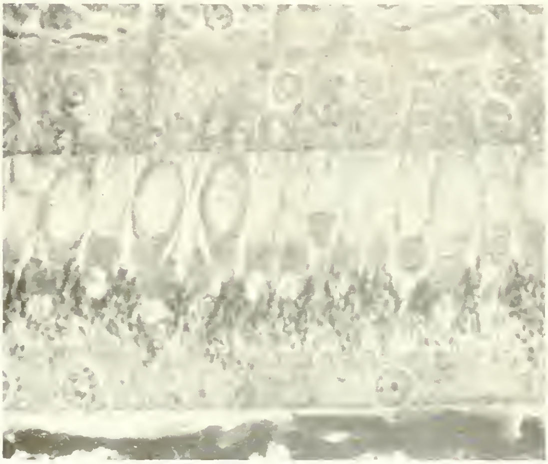


FIG. 450.—The visual cells of the tortoise (× 834) (Norman Ashton).

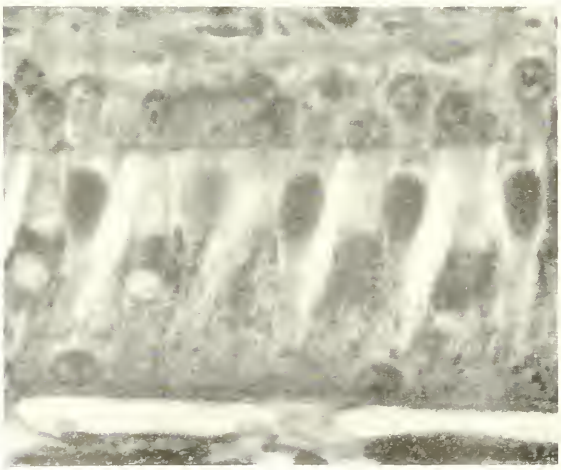


FIG. 451.—The visual cells of the Murray turtle, *Chelodina* (O'Day).

and the absence of an oil-droplet are also present ; these anomalous cells occur particularly in those species which habitually avoid the light (the snapping turtle, *Chelydra*) or are frankly nocturnal (the terrapin, *Pseudemys*) (Detwiler, 1916–43 ; Walls, 1934–42). The cones retract slightly on exposure to light (Detwiler, 1916) and, as in lizards, the migration of the retinal pigment is restricted (3·6μ in the tortoise, Detwiler, 1916).

An area centralis on the visual axis is present in the retina of most species where the cones are smaller and more densely packed than elsewhere and the increased number of nuclei determine a thickening of the nuclear layers [1] ; a fovea, however, is absent except as a rarity when a shallow depression is found.[2] In the central area the ratio of receptor cells to ganglion cells is 1 : 1, while in the periphery it is 3 : 1.[3]

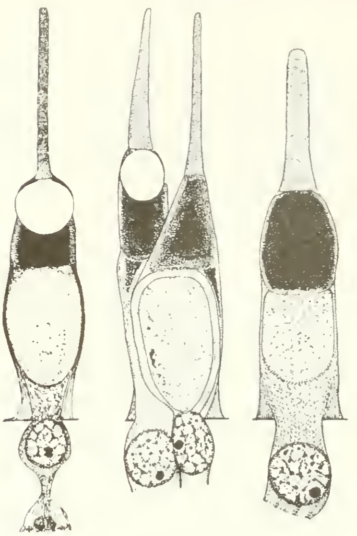
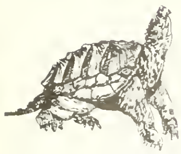


Fig. 452.—The Visual Cells of the Snapping Turtle, *Chelydra*.

A single cone, a double cone and a rod (× 1,000) (Gordon Walls).

THE OCULAR ADNEXA. Of the two lids the lower is the larger and more mobile and the palpebral aperture, horizontal in the lacertilian eye, is canted so that it runs from the dorso-temporal to the ventro-nasal quadrants of the eye, as if to make it parallel with the surface of the water in aquatic types when swimming with the head raised above the surface. Only rarely is there a transparent window in the centre of the mobile lower lid (the Murray turtle, *Chelodina* ; the turtle, *Emyda*). The movements of the lower lid and the semi-opaque nictitating membrane are controlled by two long tendons which arise from a fan-shaped PYRAMIDALIS MUSCLE fixed to the posterior aspect of the globe (Fig. 453) ; the retractor bulbi muscle is powerful and when it contracts the globe is drawn inwards and twisted far round, the lower lid and nictitating membrane covering the eye at the same time. So forceful may this movement be in some turtles that when the lower lid closes against the upper the action is continued so that the latter is pushed back into the orbit. The ocular movements, however, are relatively sluggish, the eyes moving independently of each other.



Terrapin

[1] The painted turtle, *Chrysemys*, Detwiler (1943), etc.
[2] The soft-shelled turtle, *Emyda*, Gillett (1923).
[3] The common European fresh-water turtle, *Emys obicularis*, Vilter (1949).

A harderian gland with a single duct is always present; a naso-lacrimal duct never. The lacrimal gland varies considerably. Curiously it is large in marine turtles, and may be confined to the temporal aspect of the orbit or scattered along the length of the movable lower lid with one or several ducts.

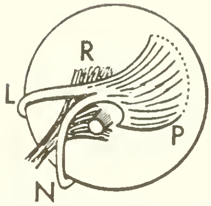


Fig. 453.—The Posterior Segment of the Globe of the Turtle.

L, tendon to lower lid; N, tendon to nictitans; P, pyramidalis muscle; R, retractor bulbi muscle (after Franz).

The orbit of the turtle is relatively small and enclosed: some of the bones common to the Vertebrates have been discarded, the nasal and lacrimal bones, for example, being replaced by the frontal.

THE CROCODILIAN EYE

THE CROCODILIA are the largest extant Reptiles, decadent survivors of the giant Reptiles which dominated the earth in Mesozoic times. Three genera are extant—the CROCODILES, widely spread over tropical rivers in Africa, Asia, Central America and Australia, the ALLIGATORS of North and South America and China, and the fish-eating GAVIALS of the Ganges River. They are sluggish creatures, more motile on water than on land where most of them obtain their prey, fond of basking in the sun and prone to hide in mud in the hot season (Fig. 454). Their eyes, primarily nocturnal in their characteristics, are adapted for aerial vision for in their predominantly aquatic activities these reptiles float with the eyes and nostrils above the surface and the rest of the body awash. Their essential features are *the absence of scleral ossicles, the reduced accommodative musculature, the slit-pupil, the marked ciliary processes, the retinal tapetum, the rod-rich retina, and the rudimentary optic nerve.*

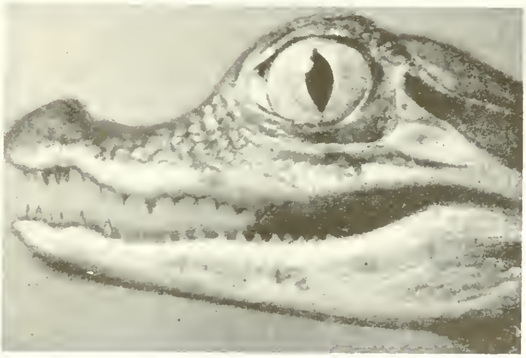
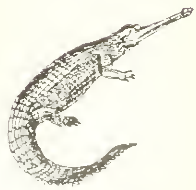


Fig. 454.—The Head of a young American Alligator of the Genus *Caiman* (R. M. Holmes).



Gavial

The EYEBALL shows the main characteristics of the typical reptilian eye described in lizards.[1] The globe, however, is almost spherical, little deformed by a corneo-scleral sulcus. The cornea is thin ; the scleral cartilage reaches almost to the ora serrata and scleral ossicles are absent.

The *ciliary body* shows more than 100 tongue-shaped ciliary processes[2] which contact the lens at its equator ; the ciliary musculature

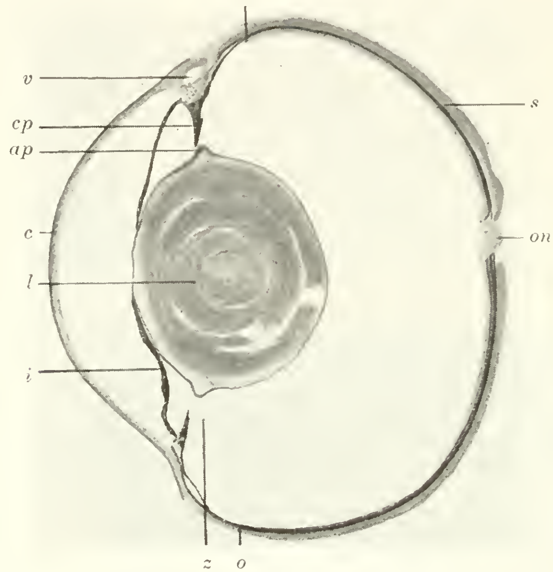


FIG. 455.—THE CROCODILIAN EYE.

ap, annular pad ; *c*, cornea ; *cp*, attenuated tongue-shaped ciliary processes ; *i*, iris ; *l*, lens ; *o*, ora serrata ; *on*, optic nerve ; *s*, scleral cartilage ; *v*, ciliary venous sinus ; *z*, position of zonule (from a drawing by Rochon-Duvigneaud, *Les Yeux et la Vision des Vertébrés*, Masson et Cie).

is represented by meridional elements only, the transversalis muscle being absent ; while the angle of the anterior chamber forms a wide cleft spanned by an unusually large pectinate ligament. In this region the branched ciliary venous sinus, the analogue of the canal of Schlemm, is wholly embedded in the sclera. The anterior surface of the *iris* is covered by a thick layer of lipophores and guanine-bearing iridocytes giving this structure a conspicuously bright lemon-yellow sheen (Plate VIII). The pupil, contrary to its behaviour in Lacertilians and Chelonians, is briskly reactive both to light and drugs (Johnson,

[1] p. 356.

[2] 110 ciliary processes : Tiedemann, Oppel and Liposchitz, *Naturgeschichte der Amphibien*, Part 1. Heidelberg (1817).

1927) ; it contracts to a vertical slit which becomes narrowed to a stenopœic slit when the animal basks in the sun. The contraction time is short, the dilatation time long (Laurens, 1923). The *lens* is ellipsoidal in shape and the annular pad small ; accommodation is slow and its range relatively small.

In the alligator the retinal epithelium is modified in the upper half of the *fundus* to form a tapetum which shines with a bright pinkish-orange glow ; in a dark-adapted eye the red shimmer of rhodopsin

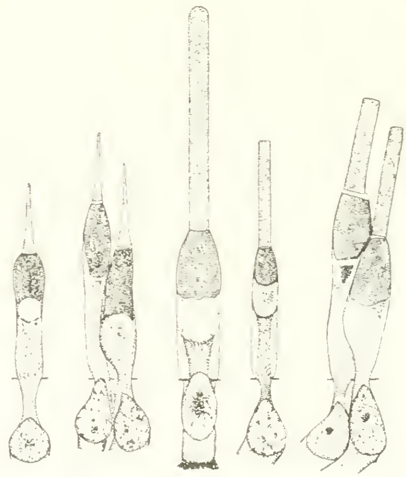
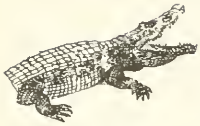


Fig. 456.—The Visual Cells of Crocodilians.

The visual cells of the American alligator, *Alligator mississippiensis*. Reading from the left, the elements are : a single cone and a double cone from the ventral fundus ; a rod ; a single cone and a double cone from the periphery of the fundus opposite the centre of the tapetum lucidum (× 1,000) (Gordon Walls).

can be seen ophthalmoscopically against the bright background rapidly fading on exposure to light, a phenomenon which provided the first demonstration of visual purple in the living eye (Abelsdorff, 1898). The retinal epithelium in the tapetal area is heavily packed with guanine crystals and does not contain sufficient fuscin in the cell-bodies or in their processes to occlude the mirror effect of the tapetum (Kopsch, 1892 ; Laurens and Detwiler, 1921).

The visual cells resemble those of the Chelonians except that oil-droplets are lacking from the cones (Fig. 456). The rods, however, greatly outnumber the cones (12 to 1 in the periphery, Verrier, 1933) and in the tapetal area the cones, both single and double, tend to assume a slender, more rod-like shape, forming, in Walls's (1934) view, a transition stage between the two visual elements. Near the ventral border of the tapetum there is a horizontally oval area centralis,



Crocodile

populated mainly by rods, in which all the visual elements are slender and more closely packed than elsewhere ; a fovea is absent.

The fundus seen ophthalmoscopically presents a uniform yellow background stippled with brownish pigment and orange dots in the centre of which is the white circular optic disc with its patch of dark moss-like pigment (Plate VIII). The retina is avascular and is nourished from the choroid ; in the crocodile a small, flat pigmented glial pad with one or two capillaries represents a rudimentary and functionless conus ; in the alligator the disc is devoid of vessels although there are a few capillaries in the optic nerve (Mann, 1929). The optic nerve is slender and elementary in structure with no septal system.

Figs. 457 and 458.—The Eye of the Alligator.

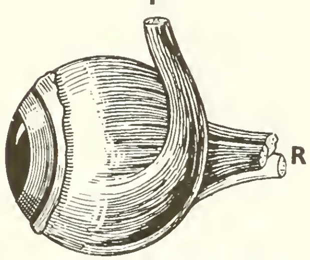


Fig. 457.—(After Bland-Sutton.)

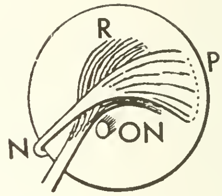


Fig. 458.—(After Franz.)

N, tendon of nictitans ; *ON*, optic nerve ; *P*, pyramidalis muscle ; *R*, retractor bulbi muscle.

THE OCULAR ADNEXA. The lids are said to be peculiar in that, alone among Reptiles, the upper is the more mobile, an observation, however, which has been questioned (Prince, 1956). This lid usually contains a tarsal plate of fibrous tissue ; it is fringed by a tough membrane split at the margin into some 20 broad pieces giving the appearance of a row of exceptionally thick eyelashes which had been glued together and then had their tips cut off. In addition there is a well-developed nictitating membrane so transparent that all the details of the iris can be seen through it with ease ; its convex free border is marked by three or four bands of brown pigment and the membrane itself is stiffened by a cartilage. It moves obliquely backwards and slightly upwards controlled directly through a long tendon by a pyramidalis muscle corresponding to that in Chelonians (Figs. 457–8). The membrane is often moved across the eye without the eyelids being closed ; and, if the eyes are closed the nictitans is first moved across, not simultaneously with the lids, as occurs in most other Reptiles. Both the harderian and lacrimal glands are well developed as are the conjunctival glands, the latter associated with the movable upper lid ;

just inside this lid there is a row of 3 to 8 puncta leading to the lacrimal duct. In *Crocodilus porosus*, however, the lower lid is lined with lacrimal glands and there is only one punctum. In all the Crocodilia these glands are said to play a relatively small part in the lubrication of the eye ; as was first pointed out by Rathke (1866) the secretion appears to pass directly down the lacrimal duct possibly with the object of lubricating the food (Leydig, 1873).

No signs of external lacrimation can be elicited even on stimulation of the eye by the instillation of such irritative solutions as the juice of an onion mixed with common salt (Johnson, 1927). It would appear that the legend of " crocodile tears " is a myth ; it will be remembered that Sir John Maunderville in his *Travels* (*ca.* 1400) accused this reptile of shedding hypocritical tears in sorrow before it devoured its victim.

The bony *orbit* is enclosed and within it the eye projects upwards so that it remains above the level of the water when the rest of the head is submerged.

THE RHYNCHOCEPHALIAN EYE

Sphenodon (*Hatteria*) *punctatus*, the New Zealand " lizard " or tuatara, is a veritable living fossil and the only extant representative of the Rhynchocephalia ; it is a small olive-green animal spotted with yellow above and white below, carnivorous in habit, living a solitary

FIG. 459.—THE TUATARA, *SPHENODON* (from Burton's *Story of Animal Life* Elsevier Pub. Co.).

nocturnal life in holes or burrows which it often shares with a petrel, and is found only in some small islands in the Bay of Plenty off the coast of the North Island of New Zealand where, however, it is tending to become extinct (Fig. 459).

The eyeball as a whole, studied originally by Osawa (1898) and later by Dendy (1910), Howes and Swinnerton (1903) and Mann (1932–33), resembles closely that of the lizard adapted for nocturnality ; its essential features are *the large cornea and lens, the reduced accommodative apparatus, the slit-pupil, the rod-rich avascular retina with few insignificant cones, and the presence of a fovea.*

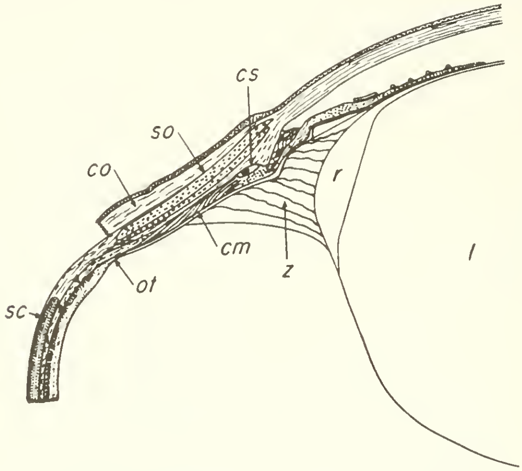


Fig. 460.—The Ciliary Region of *Sphenodon.*

A diagram from Walls showing *cm*, ciliary muscle ; *co*, conjunctiva ; *cs*, ciliary venous sinus (containing a nerve shown in black) ; *l*, lens ; *ot*, ora serrata ; *r*, annular pad ; *sc*, scleral cartilage ; *so*, scleral ossicles ; *z*, zonule.

The globe is large with a marked sclero-corneal sulcus ; the *cornea* is strongly curved with a thin two-layered epithelium ; and the sclera is provided with an extensive cartilaginous cup and a ring of 16 to 17 ossicles.

In the *choroid* there are peculiar spheroidal cells, heavily pigmented and with central nuclei, which form a dense aggregation opposite the fovea. The *ciliary body*, like that of the lizard, shows no ciliary processes, and the circular ciliary venous sinus, lying on the inner aspect of the sclera at the level of the root of the iris, is very large with an annular nerve on its posterior aspect (Fig. 460). The ciliary muscle is feebly developed. The *iris* is brightly coloured with a layer of chocolate-coloured chromatophores through the apertures of which are seen coppery lipophores and silvery iridocytes ; the vascular

THE EYES OF CROCODILIANS AND *SPHENODON*

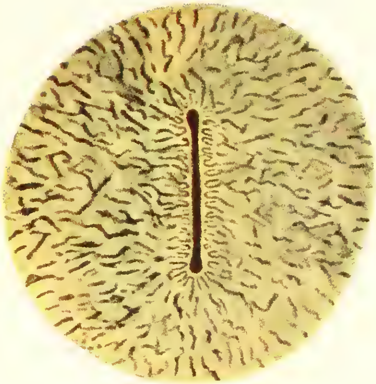


FIG. 1.—The iris of the broad-fronted crocodile, *Osteolæmus tetraspis* (Ida Mann).

FIG. 2.—The iris of the spectacled cayman. *Caiman crocdilus* (Ida Mann).

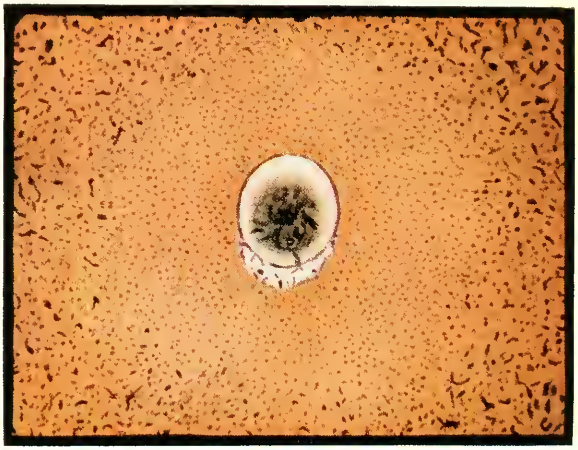


FIG. 3.—The fundus of *Alligator chinensis* (Lindsay Johnson).

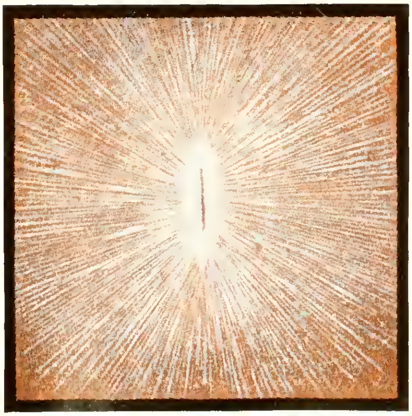


FIG. 4.—The fundus of *Sphenodon* (Lindsay Johnson).

[*To face p.* 381.

pattern comprises a system of arcades running towards the pupillary margin, some of the vascular loops of which leave the iris and float freely in the anterior chamber (Mann, 1931) (Figs. 461 and 462). The round *pupil* contracts into a vertical slit, and both circumferential sphincter and radial dilatator muscle fibres are present.

The *lens* is large, making the anterior chamber shallow ; it is more spherical than in diurnal lizards and the annular pad is well developed. The zonular fibres are peculiar in that, arising from the

FIGS. 461 AND 462.—THE IRIS OF *SPHENODON*.

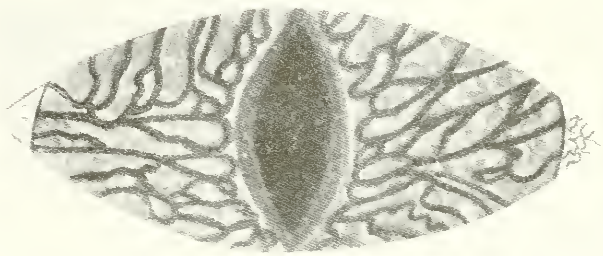


FIG. 461.—Showing the vascular arrangements (Ida Mann).

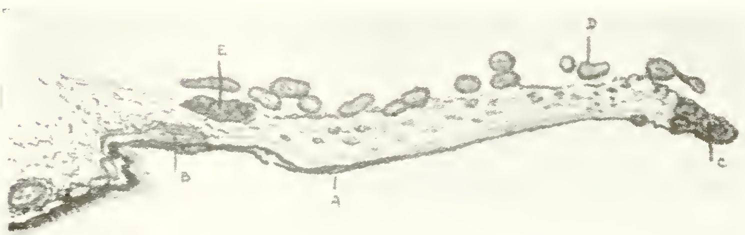


FIG. 462.—Showing the pigmentary epithelium, *A*, the sphincter muscle, *C*, and the peculiar vascular arrangements. Among these, *B* is an afferent vessel from the ciliary region, and *D* is one of the many arteries of the iris which float freely in the anterior chamber. *E* is a nerve trunk (Ida Mann).

ciliary body, they are inserted into the posterior surface of the iris as well as into the lens, as if the former tissue were impressed into the act of accommodation by being forced against the periphery of the lens to make the axial area bulge forward.[1]

The *retina* has received a considerable amount of study.[2] It is completely avascular and a conus is absent ; only a few capillaries are evident forming a network on the pale vertically elongated optic disc, to which structure they are rigidly restricted (Plate VIII). Ophthal-

[1] p. 651.
[2] Osawa (1898–99), Kallius (1898), Virchow (1901), Bage (1912), Mann (1932–33), Walls and Judd (1933), Walls (1934).

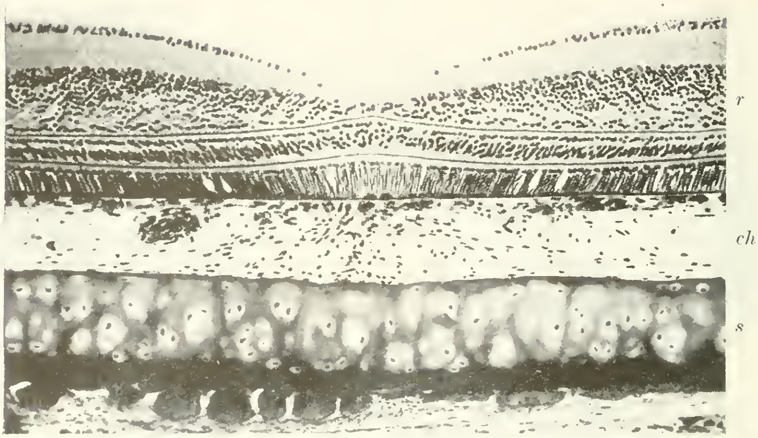


FIG. 463.—THE RETINA OF *SPHENODON* IN THE CENTRAL AREA.
Showing the shallow fovea. *r*, retina ; *ch*, choroid ; *s*, scleral cartilage (× 90) (Gordon Walls).

moscopically the fundus is reddish-brown with a stippling of golden spots whereon the arrangement of the white and relatively coarse nerve fibres is clearly delineated as they radiate uniformly outwards from the optic disc. Three visual elements are present, the majority of which were interpreted by the older writers as cones and are still held to be such by observers such as Vilter (1951) who found a relationship between the receptor and ganglion cells of 1 : 1, as in the lizard. Walls (1934), on the other hand, claimed that the preponderant visual cells are rods with enlarged and sturdy outer segments, homologous with the cones of Chelonians and Crocodilians ; single and double elements are present in approximately equal numbers, with colourless oil-droplets in the former and in one component of the latter (Walls and Judd, 1933). The third type of cell, a small and ill-formed cone without an oil-droplet, is sparse and absent from the fovea (Fig. 464). The central fovea is shallow but well-formed, and, if Walls's interpretation is accepted, shares with that of a gecko,[1] and some nocturnal primates,[2] the distinction of being the

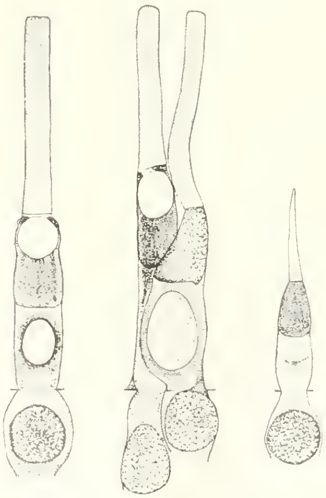


FIG. 464.—THE VISUAL CELLS OF *SPHENODON*.
A single "rod", a double "rod" and a cone (× 1,000) (Gordon Walls).

[1] p. 365. [2] p. 486.

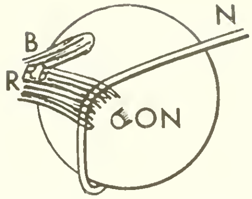


Fig. 465.—The Posterior Segment of the Globe of *Sphenodon*.

B and *R*, the two heads of the retractor bulbi muscle ; *N*, tendon of nictitans ; *ON*, optic nerve (after Franz).

only rod-foveæ in terrestrial Vertebrates (Fig. 463).[1] The *optic nerve*, like that of Crocodilians, is slender and simple in architecture without a septal system.

THE OCULAR ADNEXA resemble closely those of the lizard, but the tendon of the nictitating membrane slips round a sling formed by the unusually large two-headed retractor bulbi muscle, to find insertion into the orbital wall. The lacrimal gland is lacking but a simple harderian gland is present. In contrast to that of the lizard, the orbit is enclosed with sturdy temporal arches.

THE OPHIDIAN EYE

THE OPHIDIA (SNAKES OR SERPENTS), limbless reptiles having no pectoral and never more than a hint of a pelvic girdle, are of widespread distribution particularly in the tropics ; most are terrestrial, a few amphibious, and many habitually marine. Although many genera exist, the eyes of all snakes are very alike—apart from the Typhlopidæ, degenerate creatures generally smaller than earthworms and subterranean in habit which have vestigial eyes.[2]

Curiously, however, the ophidian eye is extremely unlike that of all other Reptiles in almost every particular. *There is no scleral cartilage or ossicles ; the iris vasculature forms an indiscriminate network and its striated musculature, ectodermal in other Reptiles, is replaced by mesodermal fibres derived from the ciliary region ; the ciliary venous sinus is corneal in location ; the lens possesses sutures and an anterior annular pad, and since it is divorced from the ciliary body, a new method of accommodation has been invented depending on pressure transmitted to the vitreous ; the retina has no conus papillaris but a membrana vasculosa retinæ ; the visual elements are distinctive and varied in their type ; and the thick optic nerve is fascicular, each bundle being provided with an axial core of ependymal cells.*

It would at first sight seem strange that the eyes of snakes should be unique and so profoundly different from those of other Reptiles, particularly lizards from which the Ophidia are directly derived. It would appear, indeed, as was suggested by Walls (1942) and maintained by Bellairs and Underwood (1951), that the first snakes, derived from burrowing lizards, lived a nocturnal existence underground during

[1] Compare the ill-formed temporal foveæ of the deep-sea Teleosts, *Bathytroctes* and *Bathylagus* which also contain rods, p. 310.
[2] p. 731.

which period their eyes lost most of the specialized adaptations found in Lacertilians and became degenerate ; on emerging again above ground it became necessary for them to be reconstituted anew so that devices of their own were invented to compensate for those lost in the dark subterranean phase of their existence. That snakes developed

Fig. 466.—The Head of the Grass Snake *Tropidonotus natrix natrix* (Katharine Tansley).

Fig. 467.—The Head of the Python, *Spilotes variegatus*. To show the spectacle (O'Day).

eyes quite unlike those of all other Reptiles is readily understandable in terms of this hypothesis. Indeed, that they approach so nearly the standard vertebrate pattern after the tremendous feat of reconstituting themselves after near-extinction is more surprising than that they differ so markedly from their near relations ; the fact that they did so is a tribute to the adaptability of the vertebrate eye and the biological utility of its general organization.

The GLOBE OF THE EYE is typically spherical or—for the first time among Vertebrates—slightly elongated in the direction of the visual axis. The *sclera* is composed entirely of connective tissue without cartilaginous or osseous supports, varying considerably in thickness among the different families but usually thinnest about the equator where it is most deformed during accommodation. Usually its outer surface is pigmented with melanophores, typically forming a dotted pattern, sometimes a continuous layer, and occasionally (*Python*) the

FIGS. 468 AND 469.—THE OPHIDIAN EYE.

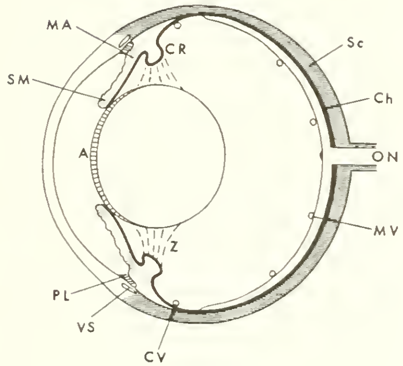


FIG. 468.

FIG. 469.

FIG. 468.—Diagram of an ophidian eye. *A*, anterior pad ; *Ch*, choroid ; *CR*, ciliary roll ; *CV*, circular vein ; *MA*, muscle of accommodation ; *MV*, membrana vasculosa retinæ ; *ON*, optic nerve ; *PL*, pectinate ligament ; *Sc*, sclera ; *SM*, sphincter muscle ; *VS*, ciliary venous sinus ; *Z*, zonule.
FIG. 469.—The eye of the tiger snake, *Notechis* (Norman Ashton).

whole thickness of the sclera contains pigment cells. The *cornea*, with its delicate single-layered epithelium protected by the "spectacle"[1] and without a Bowman's membrane, continues the arc of the sclera and usually shows a peculiar thickening at the corneo-scleral margin (Fig. 470).

The *choroid* is unusually thin, the tenuous capillary layer in most species appearing as if it were fused with the sclera (Fig. 471). The *ciliary region* starts with a narrow orbicular zone comprised of the two layers of the tall ciliary epithelium (absent in the boas: the common boa, *Constrictor*, the rubber boa, *Charina*), anterior to which the roll-like ciliary body rises abruptly as an annular fold wherein the ciliary

[1] p. 266, Fig. 279.

epithelium caps a pad of highly vascular, deeply pigmented uveal tissue (Fig. 470); from this CILIARY ROLL strands of fibrous tissue run forwards across the angle of the anterior chamber to find insertion in the peripheral corneal thickening. The circumferential ciliary venous sinus is usually corneal in location separated from the anterior chamber by connective tissue and draining backwards into the uveal veins of the ciliary region (Fig. 472). Individual variations, however,

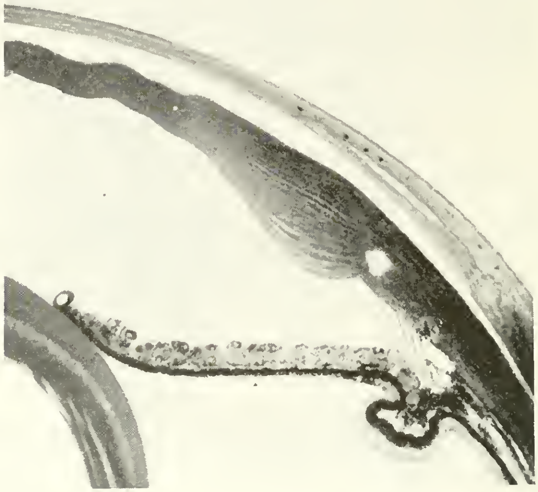


FIG. 470.—THE ANTERIOR SEGMENT OF THE EYE OF THE TIGER SNAKE.

Externally is the spectacle, *s*, beneath which the cornea, *c*, is seen with the peculiar thickening at its limbal margin. Between *s* and *c* lies the closed conjunctival sac. *l*, lens. The ciliary roll, *cr*, is a marked feature and above it is seen the pectinate ligament traversing the angle of the anterior chamber immediately above which is the large ciliary venous sinus within the corneal limbus (× 53) (Norman Ashton).

occur particularly among the Boidæ; in *Python*, for example, it is situated close to the outer surface of the cornea and drains into the subconjunctival veins, and in *Constrictor* and the sand-boa, *Eryx*, it is absent.

Cobra

The *iris* is a thick and relatively massive tissue heavily pigmented with melanophores, lipophores and iridocytes. As a rule, however, the resultant colour-scheme is relatively dull and compared with many other Reptiles the variations are small, the preponderant colours being browns and yellows sometimes with a metallic sheen; quite often the colour-pattern of the skin is continued in the eye (Plate IX).

Thus in the cobras (Elapidæ) the iris is brownish-yellow speckled with gold; in the corn-snake, *Coluber guttatus*, orange-red; in *Python*, brown with a metallic

PLATE IX

The Irides of Snakes

(Ida Mann)

Fig. 1.—Royal python. *Python regius.*

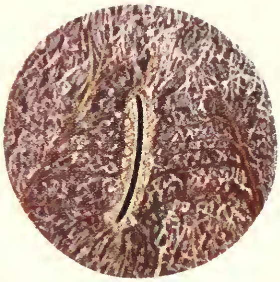


Fig. 2.—Reticulated python. *Python reticulatus.*

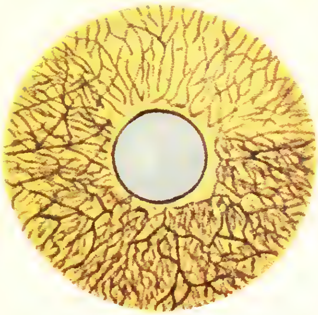


Fig. 3.—Four-line snake. *Elaphe quatuorlineata.*

Fig. 4.—Black-and-gold tree-snake. *Boiga dendrophila.* The edges of the brown and yellow scales below the eye are seen.

Fig. 5.—Emerald tree-snake, *Passerita prasina.* *A*, right eye; aphakic area on right. The outline of the lens can be seen. The green scales surrounding the eye are shown. *B*, the shape of the pupil when contracted.

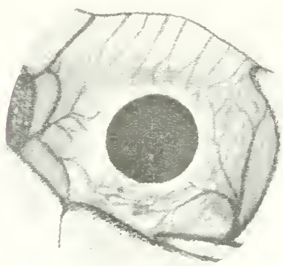


Fig. 6.—Chicken-snake. *Elaphe quadrivittata.* The edges of the scales bordering the eye are also shown.

silver sheen (Plate IX, Figs. 1 and 2). In many species a clear-cut differentiation in colour occurs—brown and gold in the king-snake, *Lampropeltis getulus*, silver and gold in the black-and-gold tree-snake, *Boiga dendrophila* (Fig. 4). A bright yellow pattern is seen in the four-line snake, *Elaphe quatuorlineata* (Fig. 3), a silver appearance in the painted tree-snake, *Ahaetulla picta*, and in the chicken-snake, *Elaphe quadrivittata* (Fig. 6).

The vascular pattern of the iris is peculiar and unique (Mann, 1931). The most primitive types (Boidæ) show a fairly well defined arrangement of vessels somewhat resembling that seen in geckos. This

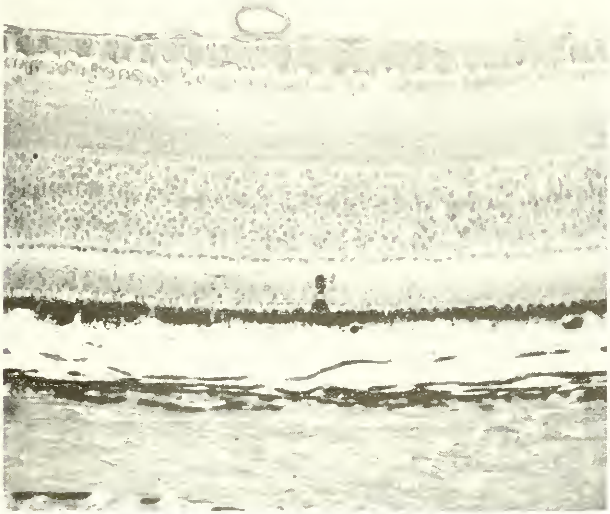


Fig. 471.—The Posterior Segment of the globe of the Copperhead Snake.

r, retina ; *p*, pigmentary epithelium ; *ch*, choroid which became detached from the pigmentary epithelium ; *s*, fibrous sclera ; *v*, a vessel of the membrana vasculosa retinæ (× 240) (Norman Ashton).

is most apparent in the pythons (Plate IX, Figs. 1 and 2) ; two main arteries enter, one on either side, and run to the pupillary aperture round which they supply a narrow circumpupillary plexus while the rest of the iris is occupied by an intermediate network of vessels. In most other snakes the walls of the vessels are opaque so that no blood-flow can be made out ; moreover, they are heavily obscured by pigment and are arranged in so haphazard a manner that the interpretation of the vascular arrangements is difficult.

Copperhead (crotalid snake)

The musculature of the iris is mesodermal and derived from the ciliary region. Circular fibres predominate, being concentrated into two accumulations, one near the pupil to form a relatively compact mass acting as a sphincter, the other at the root acting as a muscle of accommodation ; the dilatator fibres lie beneath these and run radially towards and sometimes into the ciliary body. The pupils are usually very active since they assume the light-protective function in the absence of movable lids ; in some types, however, the contraction is slight (*Python*) or even absent (the European grass-snake, *Tropidonotus natrix* ; the Madagascar sharp-nosed snake, *Heterodon madagascariensis*). Probably because of the impermeability of the corneal spectacle, the instillation of miotic or mydriatic drugs is without effect (Johnson, 1927). In nocturnal and burrowing snakes (with few excep-

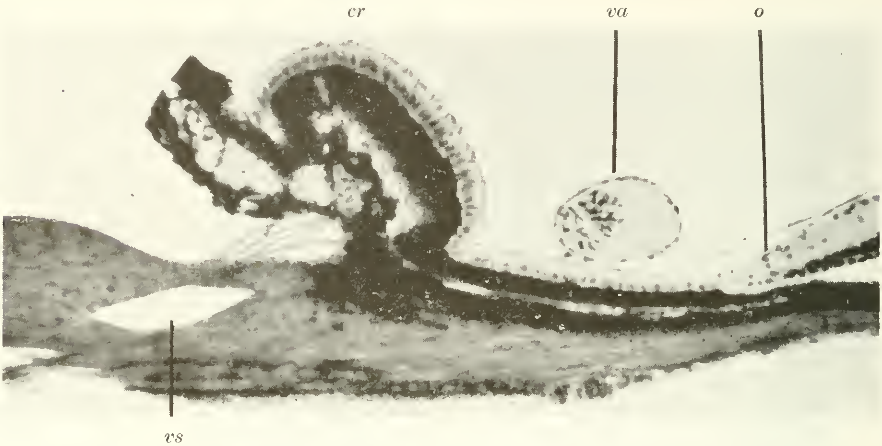


FIG. 472.—THE CILIARY REGION OF THE GRASS SNAKE, *TROPIDONOTUS NATRIX NATRIX*.

Showing *cr*, ciliary roll ; *o*, ora serrata ; *va*, hyaloid venous arc ; *vs*, ciliary venous sinus (× 108) (Katharine Tansley).

tions such as the coral snake, *Elaps*), the constricted aperture is a vertical slit or ellipse ; in diurnal types it is circular except in some Asian and African tree-snakes (Opisthoglyphs).

In these (the East Indian long-nosed tree-snake, *Dryophis*, and its relative *Dryophiops*, the African bird-snake, *Thelotornis*, and the emerald tree-snake, *Passerita*) the pupil is a horizontal slit shaped like a key-hole with the slot of the key-hole extending on the nasal side almost to the limbus, well beyond the equator of the lens. As occurs in many teleostean Fishes,[1] the pupil thus shows a phakic and an aphakic area (Fig. 808). On contraction of the pupil the central part closes completely leaving two small pupillary apertures, a larger temporal (phakic) and a smaller nasal (aphakic) aperture. It is significant that at least in some of these snakes a temporal fovea occurs and their vision is said to be very acute (Plate IX, Fig. 5).

The *lens* is subspherical (1·1–1·25), is firmer in consistency than in other Reptiles, is provided with sutures, and instead of an equatorial

[1] p. 304.

annular pad, there is a region on the anterior surface (except in Boidæ) where the subcapsular epithelial cells instead of being cuboidal are elongated to form an ANTERIOR PAD (Fig. 468). In most diurnal types the whole structure is pigmented yellow (Rabl, 1898; Hess, 1912; Walls, 1931). The zonule consists of two systems of fibres, one running from the anterior surface of the ciliary roll to the anterior surface of the lens, the other from the posterior surface of the ciliary body to the

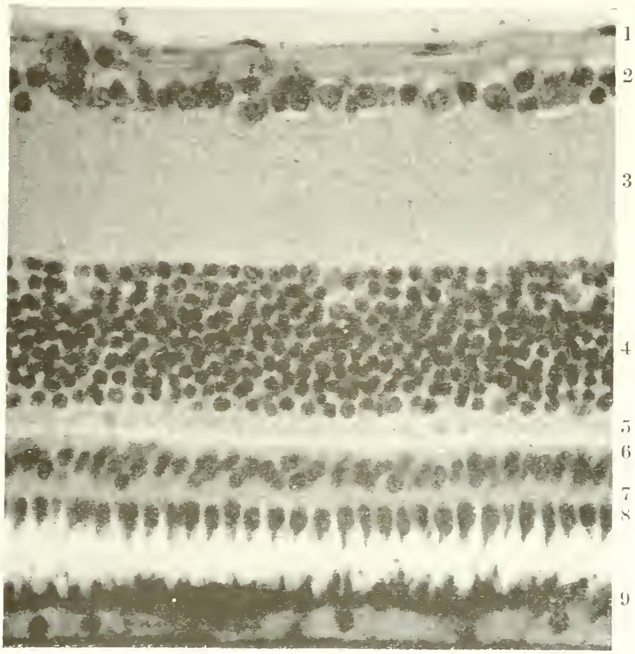


FIG. 473.—THE RETINA OF THE GRASS SNAKE, *Tropidonotus natrix natrix*.

The pure-cone retina of a diurnal snake. 1, optic nerve fibre layer; 2, ganglion cell layer; 3, inner plexiform layer; 4, inner nuclear layer; 5, outer plexiform layer; 6, outer nuclear layer; 7, external limiting membrane; 8, cones; 9, pigmentary epithelium (× 330) (Katharine Tansley).

posterior surface of the lens; except in the boa, *Epicrates*, there are no intermediate fibres attaching to the equatorial region between these two systems. Accommodation is effected by a unique mechanism quite different from that seen in other Reptiles.[1]

The *fundus oculi* seen ophthalmoscopically presents a remarkably constant picture (Johnston, 1927) (Plate X, Figs. 1 and 2). The background is grey mottled with spots, usually white (as in the corn-snake, *Coluber guttatus*) or red (as in the Boidæ), and the semi-opaque nerve fibres radiating uniformly from the optic disc are conspicuous. Occa-

[1] p. 648.

sionally, particularly in the Indian python, *Python molurus*, choroidal vessels somewhat resembling those seen in the human eye are evident in the periphery of the fundus. The optic disc is always round and white, although it varies much in size; that of the water-snake, *Tropidonotus fasciatus*, is enormous, exceeding in size that of any Vertebrate with a circular disc, even that of the whales in which the eye may reach a diameter of $5\frac{1}{2}$ inches. Usually on the surface of the disc there is some melanin pigment, sometimes in small quantity (Boidæ), sometimes associated with a cushion of mesoderm, resembling the appearance seen in Crocodilians (Beauregard, 1876; Kopsch, 1892; Leplat, 1922; Jokl, 1923). This, representing the remains of mesoderm entering with the hyaloid vessels, is functionless and is not homologous with the neuroglial conus of lizards although in certain species it may project into the vitreous to form a very similar structure (pigmented in the British adder, *Vipera berus*; colourless in the king-snake, *Lampropeltis*). The remains of the hyaloid vasculature, however, form a well-defined system of vessels, three and sometimes four of which emerge through the disc from the optic nerve. In some species these are small and are apparent only a short distance from the disc (Boidæ); more usually arteries of considerable size run nasally and temporally, drain into two venous arcs which encircle the globe in the region of the orbiculus, and combine to form a hyaloid vein which runs backwards in the fundus mid-ventrally to leave the eye at the optic disc. Over the surface of the retina lying in the vitreous there is a MEMBRANA VASCULOSA of very fine capillaries (Fig. 471) (Hyrtl, 1861; Virchow, 1901; Szent-Györgyi, 1914); only in the colubrid snake, *Tarbophis*, are these known to penetrate the retina itself.[1]

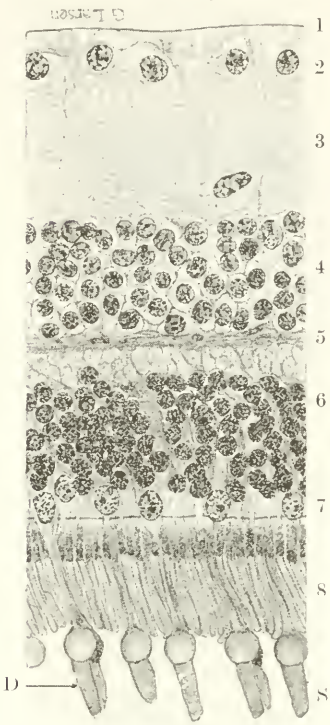


FIG. 474.—THE RETINA OF *LEPTODEIRA ANNULATA*.

The mixed retina of a nocturnal snake. 1, optic nerve layer; 2, ganglion cell layer; 3, inner plexiform layer; 4, inner nuclear layer; 5, outer plexiform layer; 6, outer nuclear layer; 7, external limiting membrane; 8, visual cells (above are rods, and below cones; D, double cone; S, single cone) ($\times$ 500) (Gordon Walls).

[1] Cf. the direct vascularization of the retina of the eel, p. 300.

PLATE X

THE FUNDI OF SNAKES

(Lindsay Johnson)

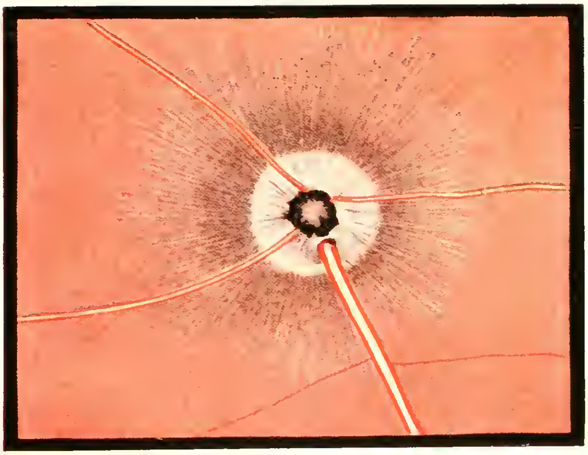


FIG. 1.—The sharp-nosed snake, *Heterodon madagascariensis*.

FIG. 2. The Indian cobra, *Naja tripudians*.

FIGS. 475 TO 480.—THE VISUAL CELLS OF SNAKES (× 1,000) (Gordon Walls).

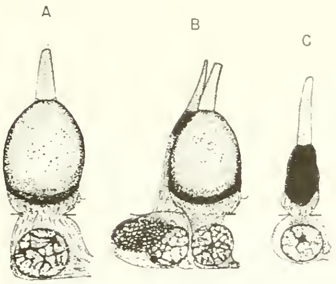


FIG. 475.—The 3 cone-types (A, B, C) constituting the fundamental pattern in diurnal forms (drawn from the European grass snake, *Tropidonotus natrix*).

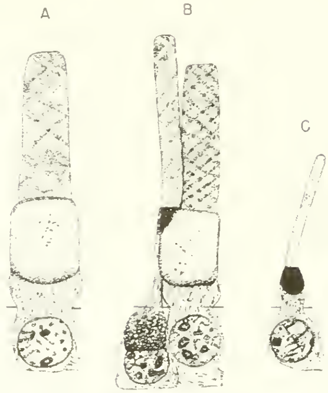


FIG. 476.—The 3 rod-types in the spotted night snake, *Hypsiglena*.

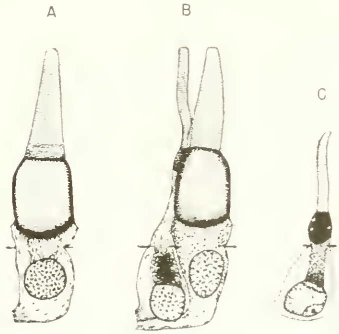


FIG. 477.—Visual cell types of scotopic colubrids.

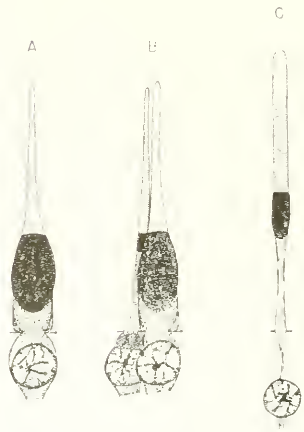


FIG. 478.—Visual cell types of the crotalids. Type C is a rod containing rhodopsin.

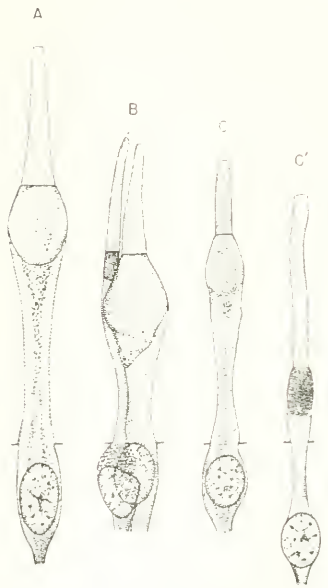


FIG. 479.—Visual cell types of the African puff-adder, *Bitis arietans* (strongly nocturnal in habit). The Type C′ (rod) is the most abundant element.

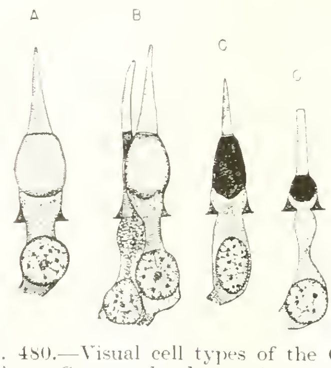


FIG. 480.—Visual cell types of the Cape viper, *Causus rhombeatus* (crepuscular in habit). There are two variations of Type C, Type C′ (rod) being most abundant.

The *retina* has the usual vertebrate structure (Figs. 473–4),[1] but the visual elements show a remarkable variation which has been most thoroughly studied and integrated by Walls (1932–42) (Figs. 475–80). In the primitive Boidæ (boas, pythons, etc.) two elements only are present, rhodopsin-bearing rods and single cones without oil-droplets or paraboloids. In most Colubridæ, on the other hand, the retina contains cones only, three types being present—Type A, a stumpy, fat, single cone ; Type B, a double cone ; and Type C with the structure of the single cones of the boïds. In diurnal colubrids and elapids (cobras), the relatively poor C-cone is eliminated ; in nocturnal varieties all three elements become more slender and in some the C-cone contains rhodopsin and becomes a rod (*Tarbophis*, the egg-eating snake, *Dasypeltis*, etc.). In the vipers (Viperidæ) the same change has occurred but some C-cones remain, while others appear as rods, four elements thus being present ; while in the Crotalidæ (rattle-snakes, moccasins) the rods greatly outnumber the cones. It is interesting that in some forms these four elements are all distinctive (the puff-adder, *Bitis arietans*) while in others (the common British adder, *Vipera berus*) the transmutation from the Type C cone to its rod-form is seen in all gradations.

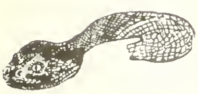
Head of *Dasypeltis*

Head of the horned viper

As we have noted, a temporal fovea occurs in certain tree-snakes (*Dryophis*) [2] and in the African bird-snake, *Thelotornis kirtlandi* (compare Fig. 807).

The *optic nerve* is primitive in its construction unlike that of all other Reptiles and resembling that of the dipnoan, *Neoceratodus*,[3] the fibres being compactly segregated by septa into fasciculi each with a central ependymal core (Prince, 1955). Afferent fibres are present, and although the majority of fibres cross at the chiasma, some uncrossed fibres are present which terminate in the lateral geniculate nucleus (*Natrix* (*Tropidonotus*) *natrix*, Armstrong, 1951 ; Prince, 1955).

THE OCULAR ADNEXA. Although snakes are popularly considered lidless, the *eyelids* are present but have fused over the eye to form a hard and horny " spectacle " [4] fitting over the globe like a contact lens and separated from the cornea by a closed conjunctival sac. This structure has excited interest from early times (Blumenbach, 1788 ; Soemmerring, 1818) and has been fully discussed by Schwarz-Karsten (1933) and Walls (1934). The nictitans, at one time assumed to form the spectacle, is absent. Embryologically, as in all Vertebrates, the lids develop as a lid-fold without commissures surrounding the eye, but in snakes this fold gradually grows over the cornea, the palpebral aperture at the same time closing and moving dorsally as it does so ; lower lid thus takes the greatest share in the process. Closure is



Head of the puff adder

Leydig (1853), Hulke (1864), Schultze (1866–67), Hoffmann (1876), Heinemann Franz (1913), Verrier (1933), Kahmann (1933).

388. [3] p. 314. [4] p. 266.

usually effected before birth, but in the uropeltid snake, *Rhinophis*, a small slit-like palpebral aperture is still present at that time. The spectacle is quite insensitive so that in time it gets scratched and dull ; Johnson (1927) found that it could be touched and even polished with a cloth in order to get a view of the fundus without any signs of inconvenience or resistance on the part of the animal, even in resentful species like the cobra or python.

When the snake sheds its skin the milky layer which forms under the stratum corneum throughout the body is very obvious through the transparent spectacle ; and with the skin the spectacle is also shed, leaving a free ragged border on its inner surface where it was attached at the sclero-corneal junction. So tough is this thin layer of skin (0·1 mm. thick) that it still retains its hemispherical form after it has been discarded ; meantime, the snake lies sluggish and irritable and seeks no food.

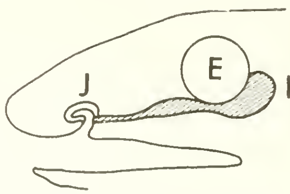


Fig. 481.—The Harderian Duct of a Snake.

E, the eye ; *H*, harderian gland ; *J*. Jacobson's organ (after Bellairs).

It is curious that in snakes the lacrimal gland (associated with the lids) is absent, but the harderian gland (usually associated with the nictitating membrane) is present. The latter is very large and its oily secretion flows into the closed conjunctival sac and from its nasal corner drains into the nose through a single naso-lacrimal duct which empties (as in lizards) inside the vomero-nasal organ of Jacobson (Bellairs and Boyd, 1947–50) ; thence it flows into the mouth where it acts as an accessory salivary secretion, lubricating the unchewed prey as an aid to the difficult act of swallowing the enormous mouthfuls of food habitual to the snake (Fig. 481).

Underneath the spectacle the eyes of snakes are freely movable, but spontaneous movements are not marked. The bursalis and retractor bulbi are absent (Nishi, 1938). The movements of the two eyes are independent except for convergence,[1] and as a general rule in order to obtain a view of an object reliance is placed on the pendulum-like movements of the head as it is swung from side to side rather than upon movements of the eyes.

Apart from the primitive boas and pythons, the *orbit* of snakes is open and fenestrated, in keeping with the general lightness of the architecture of the skull : in contrast to Lacertilians there is, however, a well-formed optic foramen. Temporal arches and a zygomatic bone are absent, probably to facilitate the wide gape of the jaws.

Abelsdorff. *Arch. Anat. Physiol., Physiol. Abt.*, 155 (1898).
Albers. *Denkschriften K. Akad. Wiss. München*, 81 (1808).
Anelli. *Ric. Morfol.*, **15**, 233 (1936).
Armstrong. *J. Anat.*, **85**, 275 (1951).
Bage. *Quart. J. micr. Sci.*, **57**, 305 (1912).

[1] See p. 695.

Beauregard. *Ann. Sci. nat. Paris* (Zool.), **4**, 70 (1876).

Beer. *Pflügers Arch. ges. Physiol.*, **69**, 507 (1898).

Bellairs and Boyd. *Proc. zool. Soc. Lond.*, **117**, 81 (1947) ; **120**, 269 (1950).

Bellairs and Underwood. *Biol. Rev.*, **26**, 193 (1951).

Blumenbach. Voigt's *Mag. für d. Neueste aus d. Physik u. Naturgesch.*, **5**, 10 (1788).

Brücke. *Arch. Anat. Physiol.*, 370 (1846).

Chievitz. *Arch. Anat. Physiol., Abt. Anat.*, Suppl., 139 (1889).

Cords. *Z. Anat. Entwick.*, **65**, 277 (1922).

Cott. *Adaptive Colouration in Animals*, London (1940).

Dendy. *Philos. Trans. B*, **201**, 227 (1910).

Detwiler. *J. exp. Zool.*, **20**, 165 (1916) ; **37**, 89 (1923).

J. comp. Neurol., **36**, 125 (1923).

Vertebrate Photoreceptors, N.Y. (1943).

Detwiler and Laurens. *J. comp. Neurol.*, **32**, 347 (1920).

Evans and Minckler. *J. comp. Neurol.*, **69**, 303 (1938).

Franz. v. Oppel's *Lhb. d. vergl. mikr. Anat. d. Wirbeltiere*, Jena, **7** (1913).

Bolk's *Hb. d. vergl. Anat. d. Wirbeltiere*, Berlin, **2** (ii), 1093 (1934).

Fritzberg. *Arch. vergl. Ophthal.*, **3**, 292 (1912).

Gillett. *Amer. J. Ophthal.*, **6**, 955 (1923).

Heinemann. *Arch. mikr. Anat.*, **14**, 409 (1877).

Hess. Winterstein's *Hdb. vergl. Physiol.*, Jena, **4**, 1 (1912).

Hoffmann. *Niederl. Arch. Zool.*, **3**, 1 (1876).

Howes and Swinnerton. *Trans. zool. Soc. London*, **16**, 1 (1903).

Hulke. *Roy. Lond. ophthal. Hosp. Rep.*, **4**, 243 (1864).

Hyrtl. *S. B. Akad. wiss. Wien.*, **43** (1861).

Johnson. *Philos. Trans. B*, **215**, 315 (1927).

Jokl. *Z. Anat. Entwick.*, **68**, 523 (1923).

Kahmann. *Zool. Jb., Abt. allg. Zool. Physiol.*, **52**, 295 (1932).

Zool. Anz., **102**, 177 (1933).

v. Graefes Arch. Ophthal., **135**, 265 (1936).

Kallius. *Anat. Anz.*, **14**, 623 (1898).

König. *Jena. Z. Naturwiss.*, **69**, 223 (1934).

Kopsch. *Iris u. Corpus ciliare des Reptilienauges*, Berlin (1892).

Krause, W. *Z. rat. Med.*, **20**, 1 (1863).

Int. Mschr. Anat. Histol., **10**, 12 (1893).

Läsk[illegible]. *Jena. Z. Naturwiss.*, **69**, 15 ([illegible]4).

Lau[illegible] [illegible]raefe-Saemisch Hb. ges. Augen-[illegible]*, Leipzig, II, **1** (2), Kap. 3 (1931).

Laure[illegible] [illegible]*mer. J. Physiol.*, **64**, 97 (1923).

Laurens and Detwiler. *J. exp. Zool.*, **32**, 207 (1921).

Leblanc. *C. R. Acad. Sci.* (Paris), **179**, 996 (1924).

Bull. Soc. Hist. nat. de l'Afrique du Nord, **16**, 49 (1925).

Leplat. *Bull. Acad. belg. Cl. Sci.*, **7**, 748 (1921).

C. R. Ass. Anat., **17**, 195 (1922).

Leydig. *Anat.-hist. Untersuch. über Fische u. Reptilien*, Berlin (1853).

Arch. mikr. Anat., **9**, 598 (1873).

Loewenthal. *Arch. Anat.*, Paris, **20**, 1 (1935) ; **21**, 315 (1936).

Mann. *Trans. ophthal. Soc. U.K.*, **49**, 353 (1929).

Trans. zool. Soc. London, **21**, 355 (1931).

Proc. roy. Soc. Med., **25**, 834 (1932).

Brit. J. Ophthal., **17**, 1 (1933).

Mercanti. *Arch. ital. Biol.*, **4**, 195 (1883).

Mertens. *Natur u. Volk*, **84**, 184 (1954).

Müller, H. *Wurzburg. naturwiss. Z.*, **2**, 139 (1861) ; **3**, 10 (1862).

Gesammelte u. hinterlassene Schriften zur Anat. und Physiol. des Auges, Leipzig (1872).

Nishi. *Hb. d. vergl. Anat. d. Wirbeltiere*, Berlin, **4** (1938).

O'Day. *Victorian Nat.*, **59**, 141 (1942).

Osawa. *Arch. mikr. Anat. Entwick.*, **51**, 481 ; **52**, 268 (1898).

Anat. Anz., **15**, 226 (1899).

v. Pfluck. *Bull. Soc. franç. Ophtal.*, **25**, 155 (1908).

Plate. *Allgemeine Zool. u. Abstammungslehre*, Jena, **2**, 675 (1924).

Prince. *J. comp. Neurol.*, **103**, 541 (1955).

Comparative Anatomy of the Eye, Springfield, Ill. (1956).

Pütter. *Graefe-Saemisch Hb. ges. Augenheilk.*, III, **1** (x) (1912).

Rabl. *Z. wiss. Zool.*, **65**, 257 (1898).

Ranvier. *Traité technique d'histologie*, Paris (1889).

Rathke. *Untersuchungen über die Entwick. der Krokodile* (1866).

Rochon-Duvigneaud. *Ann. Oculist.* (Paris), **154**, 633 (1917) ; **170**, 177 (1933).

Les yeux et la vision des vertébrés, Paris (1943).

Schultze. *Arch. mikr. Anat.*, **2**, 175 (1866) ; **3**, 215 (1867).

Schwarz-Karsten. *Morphol. Jb.*, **72**, 499 (1933) ; **80**, 248 (1937).

Soemmerring. *De oculorum hominis animaliumque*, etc., Goettingen (1818).

Szent-Györgyi. *Arch. mikr. Anat.*, **85**, 303 (1914).

Underwood. *Nature* (Lond.), **167**, 183 (1951).

Verrier. *C. R. Acad. Sci.* (Paris), **190**, 517 (1930) ; **196**, 723 (1933).

Arch. Zool., Paris, **74**, 305 (1932).

Bull. biol. France Belg., **67**, 350 (1933).

Bull. Soc. zool. France, **60**, 443 (1936).

Vilter. *C. R. Soc. Biol.* (Paris), **143**, 338, 781, 784 (1949) ; **145**, 20, 24, 26 (1951).
Virchow. *Anat. Hefte, Abt.* 2, **10**, 720 (1901).
Arch. Anat. Physiol., Physiol. Abt., 355 (1901).
Walls. *Copeia*, p. 125 (1931).
Bull. Antiven. Inst. Amer., **5**, 68 (1932).
Amer. J. Ophthal., **17**, 892, 1045 (1934).
Biol. Symposia, **7**, 203 (1942).
Walls and Judd. *Brit. J. Ophthal.*, **17**, 641, 705 (1933).
Williams and Hecht. *Science*, **122**, 691 (1955).
Zinn. *Comment. Soc. Sci. Goettingen*, **3**, 191 (1754).