

CHAPTER XI

THE EYES OF FISHES

No book on the comparative anatomy and physiology of the eye would be complete without a tribute to VICTOR JULIUS FRANZ (1883-1950) (Fig. 286). The son of a famous astronomer in Königsberg, he worked successively in Zürich, Breslau, Halle, Frankfurt, Leipzig and Jena where he occupied the Chair of Phylogeny at the Ernst-Haeckel-Haus until after the World War when, in 1946, he was relieved of his post owing to his political associations with the Nazi party. From the time he gained his doctorate thesis on the anatomy, histology and function of the eyes of Selachians in 1905, his scientific output was continuous until 1944, and included such subjects as the anatomy of the eyes of Invertebrates and Vertebrates, particularly Acrania and Fishes, the anatomy and function of the brain of Fishes, the structure and function of pigment cells, investigations into ocular functions such as phototaxis, accommodation and the light sense of a vast number of species, and a wide range of other kindred subjects. His systematic writings were also prolific, on comparative anatomy, evolutionary processes and, above all, on the structure and function of the organs of sight in the animal world.

Compared with Cyclostomes, TRUE FISHES show many and considerable advances not only in their general structure as in the presence, among other things, of jaws, limbs (fins) and an exo-skeleton of scales from which teeth are derived, but also in their eyes which are more fully differentiated.

The general configuration of the eyes of Fishes exhibits structural characteristics which might at first sight appear to be peculiarities but most of them depend on the requirements of vision in water : it is to be remembered that the vertebrate eye initially evolved as an under-water visual organ (Figs. 287 to 291).

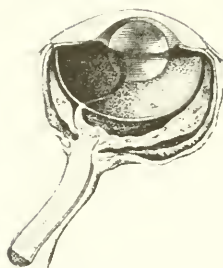
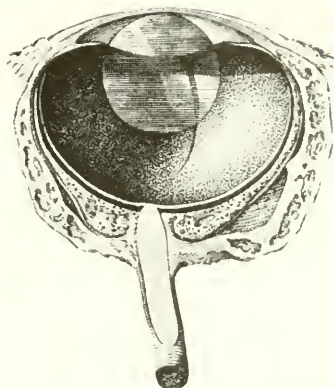
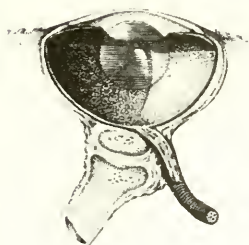
In general, the globe is large, its size tending to vary with the depth at which the animal lives ; as a rule deep-sea fishes are provided with large eyes to receive as much light as possible in these dim regions—until, indeed, the absence of light in benthonic depths leads to the degeneration of the entire organ.¹ When a change of habitat occurs during development the size of the globe may vary accordingly ; thus the sunfish, *Ranzania truncata*, spends its larval life at great depths at which stage the eyes occupy one-quarter of the area of the body, but when the adults come to spend their lives near the surface their eyes become relatively quite small in maturity. A corresponding change occurs in the eye of the eel, *Anguilla*, which grows to a relatively enormous size before it migrates from its river habitat to breed and die in the Atlantic ocean.

¹ p. 722.



FIG. 286.—VICTOR JULIUS FRANZ (1883–1950).

FIGS. 287 TO 291.—THE EYES OF TYPICAL FISHES.

FIG. 287.—The sturgeon, *Acipenser sturio* (Chondrostean).FIG. 288.—The pike, *Esox lucius* (Teleostean).FIG. 289.—The cod, *Gadus morrhua* (Teleostean).FIG. 290.—The ray, *Raja clavata* (Selachian).FIG. 291.—The dogfish, *Squalus acanthias* (Selachian).

(Reproductions of five of the beautiful engravings of D. W. Soemmerring, 1818. The reproductions are life-size and each represents the lower half of a horizontal section of the left eye.)

Vision under water requires an eye relatively hypermetropic to vision in air ; moreover, the resistance of water while swimming is considerable and, therefore, as an optical and a streamlining device particularly among actively swimming fishes, the tendency is towards a flattening of the anterior segment of the globe. The typical section

of the fish-eye is therefore ellipsoidal with the shortest diameter the visual axis (Figs. 292 and 365) ; only in sluggish forms such as the bow-fin, *Amia*, does the globe become spherical. The maintenance of a non-spherical shape in the face of changes in pressure which may be considerable necessitates a sturdy outer coat ; the sclera therefore tends to be thick and is typically reinforced with a supporting layer of cartilage sometimes supplemented by bone.

The flattening of the anterior segment implies a flat cornea ; but in a watery medium this structure is in any case useless as a refracting



FIG. 292.—THE EYE OF THE TROUT.

Note the flat shape with the short antero-posterior axis.

agent. Perfection in its optical properties is thus neglected ; it is therefore often irregular and even ridged, and in the interests of strength is frequently thin centrally and thick in the periphery giving it the construction of a sturdy arch. It follows that the entire responsibility for refraction falls upon the lens. The lens of fishes is consequently enormously large and almost spherical with a highly refractive nucleus and higher total refractive index (1.649 to 1.653) than in any other Vertebrate, making a maximal difference between it and the refractive indices of the other media. With the elimination of the cornea from the dioptric system and the dependence on the lens for refraction, it is necessary that a constant proportion should exist between the size of the lens and its distance from the retina ; Matthiessen (1886), indeed, showed that this is so, that the eyes of fishes, no matter what their size and shape, are standardized in their configuration, the distance from the centre of the lens to the retina being constant (radius of lens

$\times 2.55 = \text{Matthiessen's ratio}$). The lens has not only a light-refracting function, but in the absence of an optically effective cornea, it must also assume the onus of light-gathering. It is therefore typically situated far forward in the globe, bulging through the pupil and approximating the cornea. This large anteriorly-situated lens being an optical necessity, all other considerations of general configuration give place to it, and in cases wherein the globe would become too large to accommodate a lens of the required dimensions, as in some deep-sea types frequenting an almost lightless habitat, the shape of the eye is changed from the ellipsoidal to a tubular form so that the large lens can remain at the required distance from the retina (Fig. 380).

The large spherical lens makes accommodation by its deformation impossible, so that where an accommodative mechanism exists the expedient is adopted of moving the lens forwards or backwards—towards the cornea in the hypermetropic Selachians so that they accommodate for near vision, towards the retina in myopic Teleosts so that they accommodate for distance. The ciliary region is thus more specialized than in Cyclostomes giving rise to a suspensory apparatus for the lens and different types of muscular structures to effect these changes in its position.

The necessity of making as much use of the relatively small amount of light available in most watery habitats (apart from abyssal depths where no light is available) has led to the jacketing of the uvea of most pelagic and surface fishes with a mirror-like arrangement of guanine crystals to form the argentea, while the choroid of Selachians is provided with a tapetum lucidum; an alternative seen in certain Teleosts, is a similar deposition of guanine crystals in the pigment epithelium (the retinal tapetum).

While these form the main structural characteristics of the eyes of Fishes, other advances are seen in comparison with those of Cyclostomes, particularly the presence of an iris musculature so that the structure becomes mobile, a considerably greater elaboration of the visual cells and the retinal structure, and myelination of the optic nerve fibres and the provision of septa within the optic nerve itself.

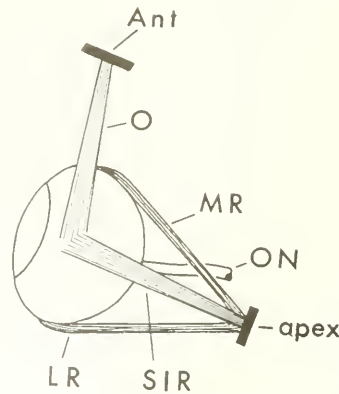


FIG. 293.—THE GENERAL SCHEME OF FISH MUSCLES (SEEN FROM THE DORSAL ASPECT).

Ant, anterior part of orbit; *apex*, apex of orbit; *LR*, lateral rectus; *MR*, medial rectus; *O*, superior (and inferior) oblique; *ON*, optic nerve; *SIR*, superior (and inferior) rectus.

As in all Vertebrates below Mammals the decussation of the optic nerve fibres at the chiasma is total.¹ An area centralis, exceptional in Selachians, is commonly seen in Teleosteans and in a number of particularly agile littoral types of this class a fovea is present.

The ocular movements in Fishes are in general restricted, reflex and primitive, and the extra-ocular muscles are essentially designed to subserve rotations of the eyes compensatory to movements of the body; with few exceptions² fixation is attained, not by movements of the eyes but of the body in swimming. The muscles are therefore designed to subserve merely the simple rotations required by the postural mechanism; the recti form a cone arising from the apex of the orbit, and the obliques, subserving simple wheel-rotations, arise anteriorly and remain on a plane anterior to the recti (Fig. 293).

The super-class of Fishes includes an enormous number of forms, many of them long since extinct; the extant types may be divided into two main classes³:

(a) CHONDRICHTHYES (χόνδρος, cartilage; ἰχθύς, a fish) (or ELASMOBRANCHS —ελασμός, a metal plate; *branchia*, a gill; so called because of their lamelliform gills) with a cartilaginous skeleton, and

(b) OSTEICHTHYES (ὀστέον, bone; ἰχθύς, a fish) with a more or less ossified skeleton.

CHONDRICHTHYES (or cartilaginous fishes) are represented today only by two sub-classes—the SELACHII (σέλαχος, a cartilaginous fish) which include the families of sharks and skates or rays, and the HOLOCEPHALI (ὅλος, whole; κεφαλή, a head), such as the *Chimaera*.

OSTEICHTHYES⁴ (or bony fishes) form a much more heterogeneous class. With the exception of the relatively modern Teleosteans, most types are largely extinct and are now represented by few species, but all of them flourished in large numbers in ancient times. The class is conveniently divided into 6 groups.

The DIPNOI (δῖς, twice; πνοή, breath) (lung- or mud-fishes) are a very ancient form abundantly represented by fossils in the Mesozoic beds throughout the world but today found sporadically as three genera only in Eastern Australia, in the marshes of Africa and the swamps of the Amazon basin. Their skeleton is largely cartilaginous and their name is derived from their double method of breathing, for their air-bladder is developed to form a breathing lung.

The CÆLACANTHINI are represented today only by one living species—*Latimeria*, a fish thought to have disappeared 80,000,000 years ago but recently discovered in the coastal seas of south-east Africa. The Cœlacanth is characterized by a skeleton, part bone, part cartilage, basal skeletal supports formed by a solid projecting lobe on which the fringe-like pectoral and pelvic fins are set.

The CHONDROSTEI (χόνδρος, cartilage; ὀστέον bone)—fishes with a cartilaginous internal skeleton—are represented today only by a few species of sturgeons and the POLYPTERINI (πολύς, many; πτερόν, a wing) which have a series of finlets instead of a dorsal fin. The latter survive as two types found in African rivers (*Polypterus* or bichir, and *Calamoichthys*). The skeleton is very bony, and the bilobed air-bladder, the duct of which opens ventrally into the pharynx,

¹ See, however, some Reptiles which form an exception (p. 392).

² p. 293. ³ p. 234.

⁴ Including Dipnoi and Teleostei this large class used to be known as GANOIDS (γανός, bony) on account of their ganoin-coated scales.

functions as an air-breathing lung. Although the Chondrostei are thus largely extinct, their descendants comprise most of the modern fishes.

The HOLOSTEI (ὅλος, whole ; ὀστέον, bone), another ancient off-shoot of the primitive Chondrosteans dating from the Permian era, are represented only by two extant species found in N. America, the gar-pike (*Lepidosteus*) and the bow-fin (*Amia*); they are characterized by the completeness of their bony skeleton.

The TELEOSTEI (τέλος, complete ; ὀστέον, bone) or modern bony fishes, probably stand in a continuous genetic line with the Holosteans and include the vast majority of fishes now alive—some 20,000 species. They date from Jurassic times, and because of their high differentiation probably began to assume their overwhelming preponderance as inhabitants of the seas in the later Cretaceous and Tertiary epochs. As would be imagined they exhibit the most fully developed and specialized eyes of all fishes.

We shall first discuss in some detail the characteristics of the eyes of the species at each end of the scale—the relatively simple eyes of Selachians and the highly developed eyes of Teleosteans, and thereafter note the essential differences in the intermediate classes.

Chondrichthyes (Elasmobranchii)

THE SELACHIAN EYE

THE SELACHIANS are divided into two orders, between which, however, the eyes differ little—(i) an older group of fusiform-shaped fishes, the EUSELACHII, comprising the sharks and their relative, the dogfish (Fig. 294), and (ii) the BATOIDEI, modified forms with flattened bodies comprising the skate-ray-torpedo group (Figs. 295 and 296). All are voracious carnivorous fishes with cartilaginous skeletons, and with few exceptions, such as the fresh-water saw-fish, *Pristis*, marine in habitat. Most of them are of benthonic habits and their eyes are therefore specifically adapted for dim illumination ; occasionally in abyssal forms which frequent the sea-bottom, the eyes have become vestigial and blind as in the deep-sea rays, *Benthobatis*, *Typhlonarke* and *Bengalichthys*.¹



Pristis

The general configuration of the eye is simple with the typical ellipsoidal shape and the scleral cartilage found generally in fishes (Figs. 297–9). The main selachian characteristics are :

a thick epichoroid on the outer surface of the choroid, somewhat reminiscent of that seen in the lamprey, and within the choroid an unusually elaborate tapetum lucidum, a structure which (unlike the tapetum of Teleosteans) has a visual function in dim illuminations ;

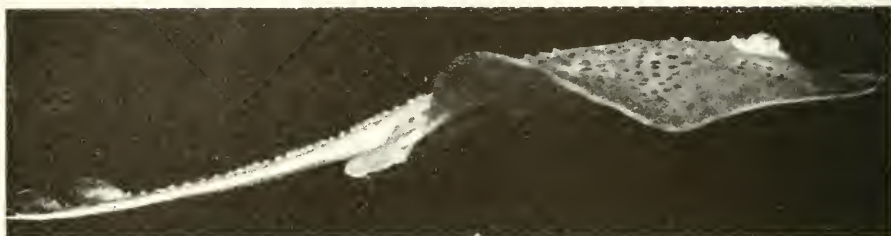
a ciliary zone provided with antero-posterior folds giving rise dorsally to a suspensory ligament of the lens and ventrally to a cushion-like papilla provided with an ectodermal protractor lentis muscle ;

a sluggishly mobile iris provided with primitive sphincter and dilatator muscles, at this stage, however, autonomously contractile and without a nerve supply ;

a shallow anterior chamber without an annular ligament (as in the lamprey), without a pectinate ligament or other structures in the free angle, and without a canal of Schlemm ;

¹ p. 724.

FIGS. 294 TO 296.—TYPICAL SELACHIAN FISHES.

FIG. 294.—The dogfish, *Scylliorhynchus canicula*.FIG. 295.—The thornback ray, *Raja clavata* (swimming).FIG. 296.—The spotted ray, *Raja montagui* (resting on the bottom) (photographs by Douglas P. Wilson).

a retina without blood-vessels (in the adult) and, with few exceptions, provided only with rods ;

an optic nerve provided with myelinated nerve fibres and, in some species, an axial core of endodermal cells resembling the arrangement in lampreys ;

a cartilaginous orbit within which the globe is supported by an optic pedicle, also of cartilage.

THE GLOBE is usually large in the sharks, smaller in the upward-looking Batoidei, and varies with the depth of the habitat—in general, the deeper the habitat, the larger the eye, as is exemplified in the enormous eyes of some deep-sea sharks (*Etmopterus*) : the dorsal eyes of rays are generally small.¹ The *cornea* is more highly curved than is seen in other fishes, and is usually oval in shape with the long axis horizontal ; it contains all the layers characteristic of the mammalian cornea with a thick epithelium derived from the skin, Bowman's and Descemet's membranes, the latter with an endothelium, and a neatly laminated substantia propria which, however, tends to become considerably thinner centrally (Strampelli, 1934 ; Loewenthal, 1938). It is pigmented peripherally in some species, particularly in its upper part, probably as a protection against light (e.g., *Torpedo*), and receives a rich nerve-supply (Shearer, 1898). The *sclera* varies considerably in thickness, being very thick in the largest sharks; the fibrous outer half is supported by a firm and complete cartilaginous cup on the inner aspect extending from the optic nerve behind to the corneal margin anteriorly (Yatabe, 1932). Sometimes this becomes calcified, and in one shark (*Laemargus*) the scleral cartilage sends large processes into the choroid.

The *uveal tract* presents features both interesting and distinctive ; it is the only vascularized tissue within the globe of the adult (Virchow, 1890). The vascular part of the choroid is typical in structure, the choriocapillaris being supplied by an artery which enters on the temporal side of the globe and drained by two main veins, one ventral and one dorsal. On its outer aspect is a heavily vascularized epichoroid of connective tissue, sometimes cavernous in its structure, particularly marked near the posterior pole so that the optic nerve has an intrachoroidal course of several millimetres. Between these two layers the centre of the choroid is occupied by the tapetum lucidum, a structure carried forwards in a much less marked form onto the anterior surface of the iris.

The TAPETUM LUCIDUM of Selachians is a remarkable structure and is found in all forms except some benthonic sharks (*Laemargus*)



Torpedo



Laemargus

¹ The dorso-lateral eyes of the eagle-ray, *Myliobatis*, are, however, quite large.

FIGS. 297 TO 299.—SELACHIAN EYES.

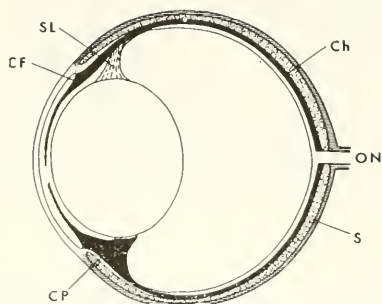


FIG. 297.—Diagram of a Euselachian eye.

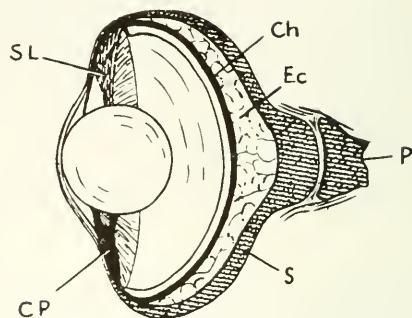


FIG. 298.—Diagram of a Batoid eye.

CF, ciliary fold ; Ch, choroid ; CP, ciliary papilla ; Ec, epichoroid ; ON, optic nerve ; P, optic pedicle ; S, sclera with complete cartilaginous cup ; SL, suspensory ligament.

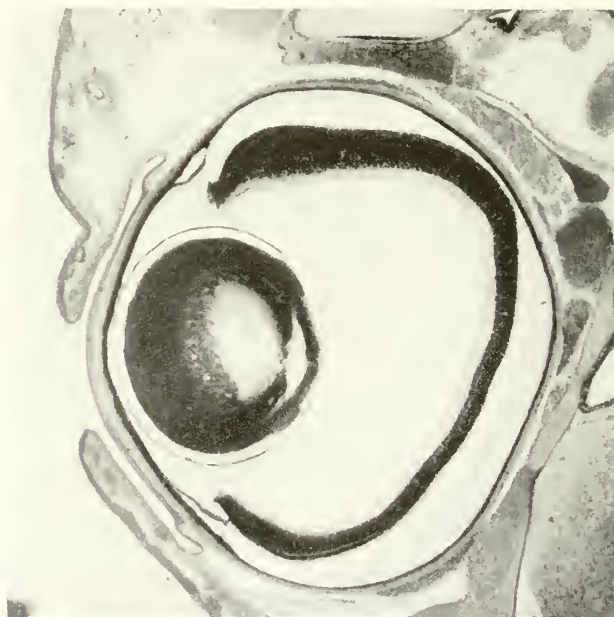
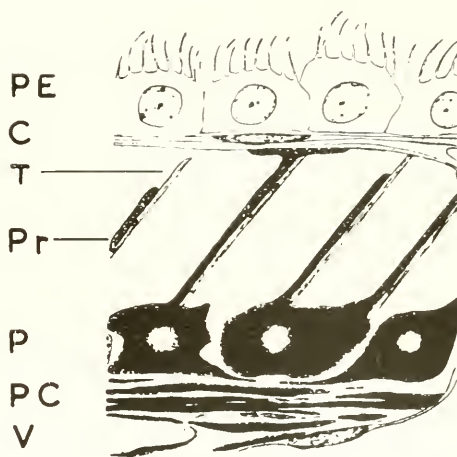


FIG. 299.—The eye of the dogfish.

The retina has been torn at the ora and the uvea detached in the ciliary zone. In the section the iris seems to adhere to the back of the cornea. Note the great thickness of the corneal epithelium and the well-formed eyelids ; the latter feature is unique to Selachians among Fishes ($\times 20$) (Norman Ashton).

and rays (*Myliobatis*) and the basking shark (*Selache maxima*). It was known to Soemmerring (1818) and has been most fully studied by Franz (1905-34). Structurally it is made up of two elements, highly reflecting cells packed with guanine crystals, and heavily pigmented melanophores. In some species such as the porbeagle shark, *Lamna cornubica*, the guanophores lie in parallel layers, the interstices between them being occupied by melanophores. In the more typical arrangement, however, the flat silvery guanophores are arranged as a series of plates running in a slanting direction to the choriocapillaris, and over them the chromatophores send pigmented processes. The arrangement as depicted by Franz is seen in Fig. 300. In dim illumination the pig-

*Myliobatis**Selache*FIG. 300.—THE TAPETUM LUCIDUM OF THE DOGFISH, *MUSTELUS*.

In vertical section, from the dorsal part of the fundus.

C, choriocapillaris; PE, pigment epithelium; PC, pigmented layer of the choroid; V, vessels of the choroid; P, pigmented cells, the processes of which (Pr) migrate over the tapetal plates (T) (after Franz, 1931).

mentary processes are retracted and the guanophores appear as a silvery row of plates like the tiles on a roof from which the incident light is reflected back to the retina; in bright illumination the pigmented cells send down their migratory processes which cover the guanophores so that all the incident light reaching the choroid is absorbed.

The *ciliary zone* of Selachians has some unique features. It is thin and without musculature, occupying a broad belt between the retina and the iris, consisting from without inwards of three layers—a mesodermal layer, the forward continuation of the choroid, a pigmented ectodermal layer, the forward continuation of the pigmented retinal epithelium, and a non-pigmented ectodermal layer, the forward

*Lamna*

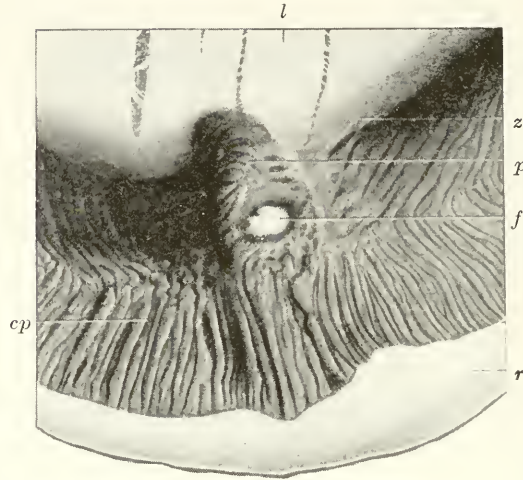
FIGS. 301 AND 302.—THE CILIARY PAPILLA OF THE DOGFISH, *SCYLLIORHINUS*.

FIG. 301.—The lens, *l*, is seen resting on the papilla, and the filaments of the zonule, *z*, are seen running from it towards the ciliary region. The papilla, *p*, is much larger than the ordinary ciliary processes, *cp*, and the small white area at its apex represents the remains of the foetal fissure, *f*. *r*, retina.

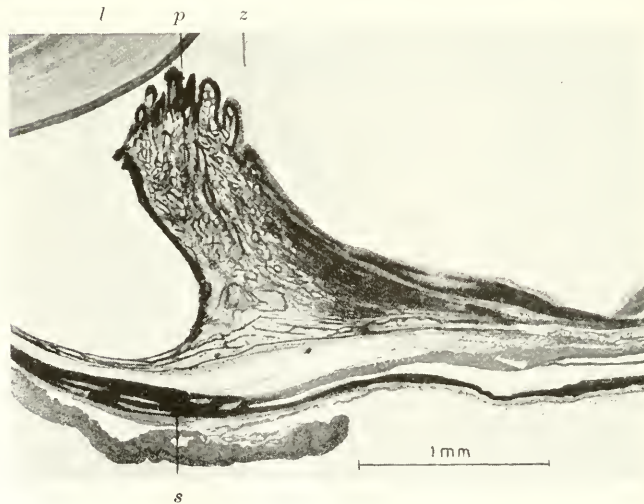
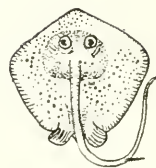


FIG. 302.—Drawing of a section through the ciliary papilla. The papilla, *p*, is seen approximating the lens, *l*. *s*, sclera; *z*, zonular fibres.

(Drawings from Rochon-Duvigneaud, *Les Yeux et la Vision des Vertébrés*, Masson & Cie.)

continuation of the retina. Anteriorly its inner surface is broken by low *ciliary folds*¹ which run in an irregularly radial direction onto the posterior surface of the iris, a formation restricted in some species of rays to the dorsal and ventral quadrants. A gelatinous disc-like *zonule* runs from the coronal region of the ciliary body to the lens near its equator, augmented in the mid-line dorsally by a firmer *suspensory ligament*, and ventrally (in most species) by a cushion-like *ciliary papilla* upon which the lens rests. The zonule and the suspensory ligament are essentially condensations of the anterior part of the vitreous (Teulières and Beauvieux, 1931). The ciliary papilla, which develops in the lips of the foetal fissure of the invaginating optic vesicle, resembles a hypertrophied ciliary fold, and is continued for some distance onto the back of the iris (Figs. 301-2); it is said to contain smooth muscle fibres, presumably of ectodermal origin, derived from the retinal layer of the ciliary body, so orientated that it acts as a *protractor lentis muscle*, which on contraction would pull the lens forwards on accommodation (Franz, 1931). It would appear, however, that such fibres are scanty and their presence has been denied (Verrier, 1930 ; Rochon-Duvigneaud, 1943).²

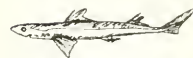
The *iris* is thin but usually extensive, being bowed forwards over the protruding lens. Both ectodermal layers are pigmented near the pupillary margin, but towards the ciliary body the posterior layer usually loses its melanin content ; pigmentation of this layer is therefore more extensive than in the case of Cyclostomes, and in some species the whole of this layer is pigmented (some sharks—*Lamna cornubica*—and rays—*Trygon*, etc.) as is the case in Teleosteans and higher Vertebrates. From the anterior layer are developed the SPHINCTER and DILATATOR MUSCLES of the pupil which have received considerable study (Franz, 1905 ; Grynfeldt and Demelle, 1908 ; L. Carrère, 1923). They are comprised of long, spindle-shaped ectodermal cells which, acting autonomously and directly through the stimulus of light, undergo sluggish and delayed contractions (Brown-Séquard, 1847-59 ; Young, 1933) ; they are more primitive than those of higher vertebrate types in that the elongated myo-ectodermal cells never leave their parent epithelial layer. It is interesting that in some sharks and dogfishes prolonged exposure to light may lead to a state of "mydriatic rigor" wherein the pupil remains permanently fixed (*Mustelus*, *Squalus*). The mesodermal layer of the iris is thin, containing vessels and chromatophores in its deeper aspects, and in its anterior parts, guanine-laden cells, not, however, arranged in packed parallel layers as is the argentea of Teleosts, but in sufficient numbers to give the iris a distinctly metallic sheen. In the angle of the anterior



Trygon



Mustelus



Squalus

¹ See footnote, p. 267.

² p. 647.

chamber there are ill-developed sinuses lined by endothelium (Rochon-Duvigneaud, 1943) ; it may be that these allow the escape of aqueous humour when the lens is pulled forward towards the cornea in accommodation.

The *pupillary aperture* varies and is largely determined by the

FIGS. 303 TO 313.—THE PUPILS OF SELACHIANS.



FIG. 303.—The angel shark, *Squatina*.



FIG. 304.—The school shark, *Galeorhinus*.



FIG. 305.—The gummy shark, *Mustelus antarcticus*.



FIG. 306.—The nurse shark, *Ginglymostoma*.



FIG. 307.—The dogfish, *Mustelus canis*.



FIG. 308.—The carpet shark, *Orectolobus*.



FIG. 309.—The leopard shark, *Triakis*.



FIG. 310.—The white-tip shark, *Carcharodon*.



FIG. 311.—The crested Port Jackson shark, *Heterodontus*, pupil dilated and contracted.



FIG. 312.—The fiddler ray, *Trygonorrhina*, pupil dilated and contracted.



FIG. 313.—The pupil of the dogfish, *Scylliorhinus*. Showing stages of contraction (after Franz).



Heterodontus

arrangement of the musculature of the iris ; when this forms a continuous sheet a round or oval pupil results ; where this is lacking in certain areas an operculum is formed (Grynfeltt and Demelle, 1908). Of the first type, some deep-sea species (the luminous shark, *Etmopterus*; *Centrophorus calceus*) have large, round, almost immobile pupils with poorly developed muscles—a configuration to be expected in their dimly lit habitat. Species which come to the surface and bask have contractile pupils, usually circular in dilatation and elliptical on contraction (characteristically in the vertical direction but sometimes oblique or

horizontal)¹ (Figs. 303 to 312). Amongst fishes this shape of pupil is characteristic only of Selachians. An expansible OPERCULUM, a structure described by Cuvier (1805) and subsequently by Leuckart (1875), is a feature of the flattened Batoidei with their upward-looking eyes²; it is a structure on the upper part of the pupillary margin which expands downwards in bright light to block the aperture so that the eyes appear to "close." The mechanism whereby this non-muscular structure contracts and expands is unknown. These opercula are of varying shapes: thus the contracted pupil of the electric ray, *Torpedo*, or the spotted dogfish, *Scylliorhinus*, is a horizontal slit divided in the middle by a tiny operculum (Fig. 313); the operculum may be provided with a smooth edge, as in the sting-ray, *Trygon*, and *Torpedo*, or the margin may be serrated as in other members of the ray family (*Raja clavata*, *R. batis*, *Trygonorrhina* and others), so that on full expansion it reduces the pupil to a crescent of stenopœic apertures (Fig. 312).

The voluminous *lens* is never completely spherical as in Teleosteans, but is always lenticular in shape with the transverse diameter slightly greater than the antero-posterior. Unlike the cyclostome lens and as occurs in all other Vertebrates except lizards, a system of sutures is present; it is, however, very simple consisting merely of a single line-suture running vertically in the anterior part and horizontally in the posterior³ (Rabl, 1898) (Fig. 314). The epithelium clothing the anterior surface is continued behind the equator, whereafter, as in other Vertebrates, the cells are prolonged into fibres, the nuclei of which lie in the posterior cortex. The *vitreous* is of a dense consistency particularly in its anterior parts where it forms the suspensory apparatus of the lens; it has little adherence to the retina posteriorly whence it is readily detached.

The *retina* has received a considerable amount of study.⁴ In the embryo, blood vessels lie in the foetal fissure (de Waele, 1900) but these disappear and in the adult the retina is quite avascular and shows no trace of the foetal fissure except a tiny white area on the summit of the ciliary papilla (Fig. 301). The retinal epithelium is comprised, as is



Scylliorhinus



Raja

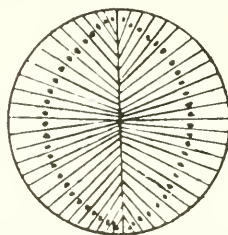


FIG. 314.—LENTICULAR SUTURES OF SELACHIANS.

Showing the vertical anterior suture. Posteriorly there is a short horizontal suture.

¹ The basking shark, *Selache*; the spiny dogfish, *Squalus*; the porbeagle shark, *Lamna*; and so on.

² Thus it is absent in the devil-fish rays, *Mobulidae*, which have lateral eyes and also in the dorso-lateral eyes of *Myliobatis*.

³ A single line-suture is found also in the lenses of most Teleosts, Anurans, Reptiles, some Birds and the rabbit.

⁴ Krause, 1886-89; Neumayer, 1897; Schaper, 1899; Greeff, 1899; Addario, 1903; Retzius, 1905; Schnaudigel, 1905; Franz, 1905; Verrier, 1930; and others.

usual, of a single layer of hexagonal cells, but when a tapetum is present these are unpigmented until the ora is reached in order to allow the passage of light to this structure (Fig. 315). The architecture of the retina itself is simple with the usual layering, but a considerable scattering of cells outside the confines of their layers may occur. The horizontal cells are unusually massive (like those of the lamprey) and ganglion cells are sparse. Characteristically the retina is pure-rod, the

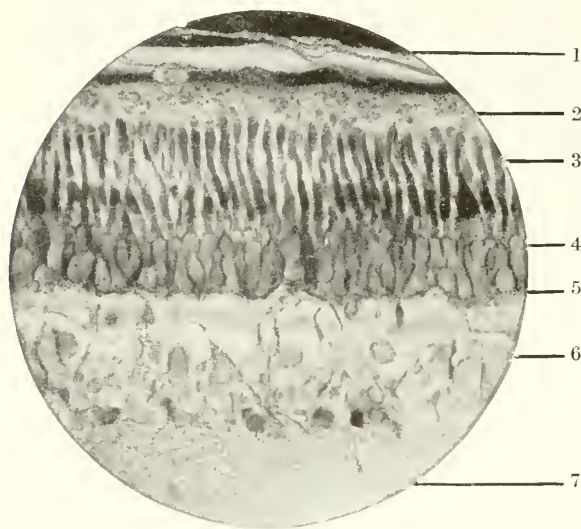


FIG. 315.—THE SELACHIAN RETINA.

The retina of the ray, *Raja maculata*. 1, pigment of choroid; 2, (non-pigmented) retinal epithelium; 3, layer of rods; 4, external limiting membrane; 5, outer nuclear layer; 6, inner nuclear layer; 7, nerve fibre layer (Mallory's triple stain) (Katharine Tansley).



FIG. 316. — THE CONE AND ROD OF THE DOGFISH, *MUSTELUS* ($\times 1000$) (Gordon Walls).

cells being thin and long; the ratio of visual to ganglion cells varies ($152 : 1$ in *Etmopterus*, $14 : 1$ in *Myliobatis*, $12 : 1$ in *Raja miraletus*—Verrier, 1930). There is no area centralis, although in some species, particularly the dogfish, *Mustelus*, the density of the visual elements is increased in a round central area so as to suggest an elementary precursor of this characteristic of the higher Vertebrates (Franz, 1905) (Fig. 317). Only in a few particularly active species are cones found—the dogfish, *Mustelus*, the eagle-ray, *Myliobatis*, and the angel-shark, *Squatina* (Franz, 1905; Verrier, 1930; Rochon-Duvigneaud, 1943) (Fig. 316).

The optic nerve has various septal patterns and in some species an endymal core, as in lampreys (Prince, 1955); like the retina it is avascular. The optic disc is small and flat and a lamina cribrosa is



Squatina

lacking. Unlike those of the lamprey, the optic nerve fibres have become myelinated (Bruesch and Arey, 1942). At the chiasma there is a complete crossing of the nerve fibres, frequently in the form of interlacing bundles (Figs. 318 and 319) (Verrier, 1930).

THE EXTRA-OCULAR STRUCTURES. The presence of mobile *eyelids*, both upper and lower, sometimes with an additional fold constituting

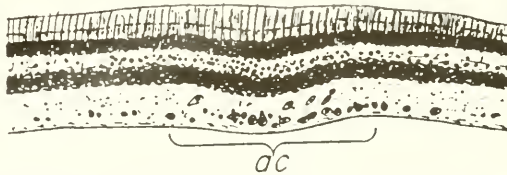


FIG. 317.—THE AREA CENTRALIS (*ac*) OF THE DOGFISH, *MUSTELUS*.

Note the increase in length and concentration of the visual cells and the great number of ganglion cells (after Franz).

a third or *nictitating membrane* in many selachian species is a curious anomaly in the eyes of a fish (Fig. 299). These structures are supplied with an elaborate musculature blended with the muscles of the spiracle; a superficial layer comprises a retractor palpebræ superioris and a constrictor spiraculi, and a deep layer consists of a levator palpebræ nictitantis, a depressor palpebræ superioris and a dilator spiraculi, the

FIGS. 318 AND 319.—THE CHIASMA OF SELACHIANS (Verrier, 1930).

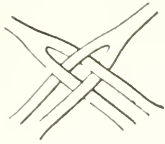


FIG. 318.—The dogfish, *Squalus*.

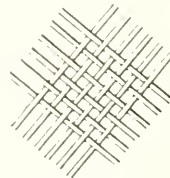


FIG. 319.—The skate, *Raja*.

different elements being more or less blended. The palpebral muscles are supplied by the seventh nerve, the muscles of the nictitating membrane by the maxillo-mandibular division of the trigeminal (Ridewood, 1898 ; Harman, 1899–1903). The lids are well developed in the deep-sea sharks of the requin family (*Galeorhinus*) wherein the outside of the nictitating membrane is clothed with the same type of minute placoid scales as is the outer surface of the lower lid. Occasionally there is merely an immobile circular lid-fold in which case a nictitating membrane alone is present (the bonnet shark, *Sphyrna tiburo*). The purpose of these elaborate lids is difficult to imagine ; Franz (1905) concluded that they were not used to escape from the dazzling of bright light.

The *orbit* is cartilaginous and usually very incomplete ; in it the eye lies in a bed of gelatinous connective tissue rich in blood sinuses. The extra-ocular muscles are simple—four recti form a cone inserted into the globe about its equator while the two obliques, arising close together, sweep round the anterior part of the globe in front of the recti and are inserted in common with the vertical recti. These muscles may be enormously developed in the larger sharks ; in the basking-shark, *Selache*, for example, they are as thick as the biceps of the average man. The most characteristic structure in the orbit, however, is the peculiar OPTIC PEDICLE, a prop-like cartilaginous structure which runs from the cranium to the posterior pole of the eye which it receives



FIG. 320.—The head of the rabbit-fish, *Chimæra monstrosa* (Bland-Sutton's *Lectures and Essays*, Heinemann).

in an expanded cupped head, thus forming a simple ball-and-socket joint (Figs. 290 and 298). The globe in its cartilaginous sclera thus receives a firm support. Sometimes the pedicle is firm and stiff ; in some sharks and rays it is slender, bending when the extra-ocular muscles contract, straightening and proptosing the eye when these relax. Sometimes it is incomplete, either not reaching the eye or the cranium (in the elongated orbit of the hammerhead shark, *Sphyrna zygaena*) (Fig. 387), or indeed, may be lacking (the spotted dogfish, *Scylliorhinus*).

THE HOLOCEPHALIAN EYE

THE HOLOCEPHALIANS are represented today only by the Chimæras (rabbit-fishes or ghost-sharks), somewhat shark-like fish of wide distribution and very primitive in type (Fig. 320) ; they are all deep-sea bottom fishes, and their eyes, which are of the same type as the selachian eye, are remarkable for their adaptation to the dim illumination of the ocean depth. For this reason the pupils are large, round and almost immobile, a tapetum is lacking, and the retina has an unusually dense population of rods summated by an unusually small number of ganglion cells (100,000 rods per sq. mm. and 600 ganglion cells, Franz, 1905)—a ratio not exceeded amongst Selachians except in the abyssal forms such as the luminous shark, *Etmopterus*. The shape of the eye is the typical ellipsoid of the selachian eye but, curiously, the sclera is thin, sometimes apparently discontinuous.

Osteichthyes

THE TELEOSTEAN EYE

TELEOSTEANS are a huge and diversified class which comprises the great majority of modern fishes. Ocularly—and in many other respects—they show the highest differentiation among fishes, exhibiting many anatomical and physiological characteristics which are peculiar to themselves.

FIGS. 321 AND 322.—TYPICAL TELEOSTEAN FISHES.



FIG. 321.—The carp, *Cyprinus* (photograph by Michael Soley).

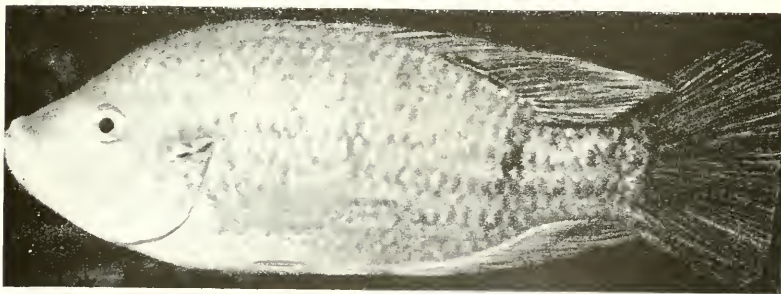


FIG. 322.—The mouth-breeder cichlid, *Cichla* (Zool. Soc., London).

Although there are great variations among the many species, the teleostean eye has certain essential characteristics (Figs. 323-4) :

an incomplete cup of hyaline scleral cartilage, and a tendency to multi-layering of the cornea ;

a very elaborately developed annular ligament bridging the angle of

the anterior chamber between the cornea and the iris, and a tensor choroidæ muscle ;

the presence of a choroidal gland in most species ;

a failure in closure of the foetal fissure allowing the protrusion of the choroid through the retina as the falciform process (or alternatively the emergence of a hyaloid system of vessels) to nourish the inner layers of the retina, which with one known exception (the eel) is avascular ;

an ectodermal retractor lentis muscle at the distal end of the falciform process ;

the frequent presence of a choroidal tapetum (argentea) usually of the lucidum type, but sometimes cellular, neither type, however, having a visual function since they are masked by the pigment epithelium of the retina ;

a pupil usually immobile and often so large as to leave an aphakic aperture ;

a highly organized retina typically containing both rods and cones as well as double cones, and sometimes a fovea.

THE GENERAL SHAPE OF THE TELEOSTEAN EYE usually conforms to the standard type characteristic of Fishes ; in most species it is an anteriorly flattened ellipsoid with the antero-posterior diameter shorter than the transverse, although in slow-swimming and small-eyed types the shape tends to be more nearly spherical.

An exception to this occurs in certain deep-sea Teleosts. In these dark regions the poverty of the illumination requires an immensely large lens, to accommodate which the globe may acquire a tubular shape.¹ Other benthonic Teleosts, giving up the struggle to make use of light in their dark environment, have vestigial eyes, often covered with opaque skin²—one deep-sea Teleost (the only known Vertebrate in such a case) has no eyes (*Ipnotops*) ; as an accessory, certain benthonic fishes have developed luminous organs, sometimes in association with their eyes, with which they make contact with their kind.³



Carassius

The sclera is a fibrous tunic sometimes tenuous and thin (as in the goldfish, *Carassius auratus*), sometimes immensely thick (the star-gazer, *Astroscopus*), reinforced by hyaline cartilage which sometimes becomes partly ossified (Yatabe, 1932 ; Rochon-Duvigneaud, 1943 ; Woelfflin, 1955) : only in a few forms is cartilage lacking (some eels, Gymnotidæ ; the pearl-fish, *Encheliophis*). Instead of forming a complete cup as in Selachians, however, the cartilage is lacking in the posterior part ; the general arrangement is therefore the opposite to that which occurs in Birds in which the posterior segment of the sclera is reinforced by cartilage (Fig. 327).⁴ Its extent varies considerably ; sometimes it is confined to a relatively narrow ring around the limbus (the salmon-trout family, Salmonidæ) or the equator ; sometimes it clothes the

¹ p. 332.

² p. 722.

³ p. 736.

⁴ p. 403, Fig. 496.

FIGS. 323 AND 324.—THE TELEOSTEAN EYE.

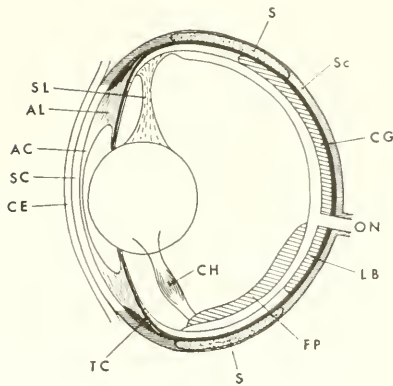


FIG. 323.—Diagram of a Teleostean eye.

AC, autochthonous layer of cornea ; AL, annular ligament ; CE, corneal epithelium ; CG, choroidal gland ; CH, campanula of Haller ; FP, falciform process ; LB, lentiform body ; ON, optic nerve ; S, scleral cartilage ; Sc, sclera ; SC, scleral cornea ; SL, suspensory ligament ; TC, tensor choroideæ.

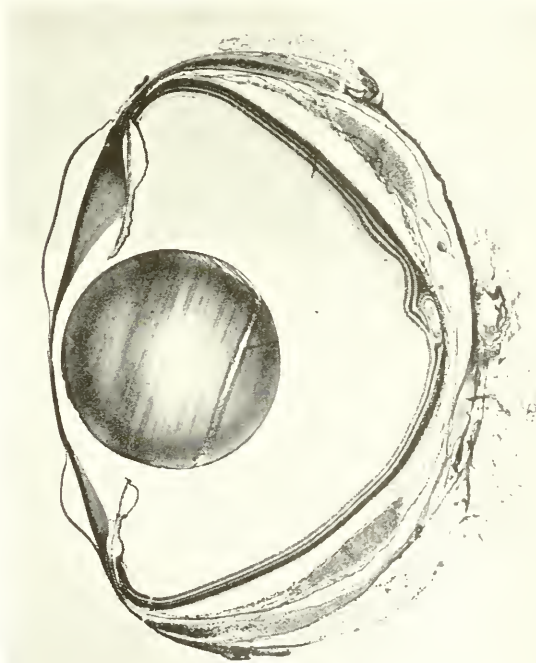


FIG. 324.—The eye of the trout. In the section the dermal layer of the cornea has come loose, as usually occurs (Norman Ashton).



Mormyrid

entire eye apart from a small fibrous zone around the optic nerve (the soles, *Soleidæ*) : sometimes it forms discontinuous islands (the elephant-fish family, *Mormyridæ*) : sometimes it becomes partially calcified, and exceptionally, as in *Tetragonopterus*, this transformation is complete. Scleral ossicles formed of true bone are also usually found, typically as thin plates embedded in the fibrous tissue of the sclera, situated temporally and nasally anterior and external to the cartilage ; occasionally in active types with large eyes these combine to form a complete osseous ring of considerable strength (the sword-fish, *Xiphias* ; tunny, *Thunnus*).¹

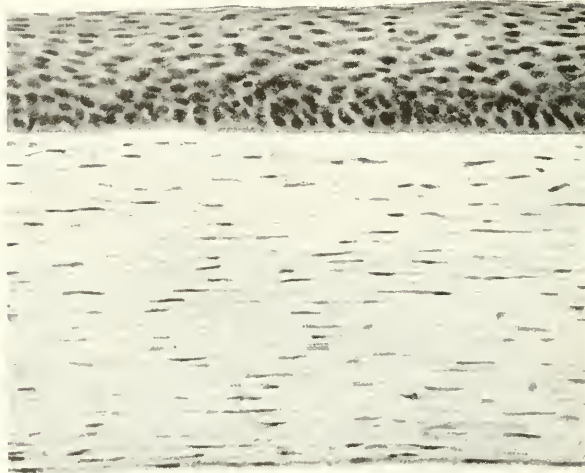
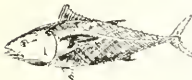


FIG. 325—THE CORNEA OF THE CARP.
Showing the thick epithelium (Smelser and Chen).

The *cornea*, usually elliptical with the long axis horizontal, (Grynfeldt, 1910 ; Verrier, 1927), is frequently irregular and grooved and has a variable constitution. In some forms it shows the usual vertebrate configuration, the substantia propria being relatively homogeneous (*Salmonidæ*—salmon, trout ; *Cyprinidæ*—minnows and eel ; *Esoeidæ*—pike) (Fig. 325) ; but in others it is uniquely complex, 4 layers being readily distinguishable :

(1) A dermal layer, derived from and continuous with the skin, consisting of a multi-layered, usually thick epithelium, Bowman's membrane and the superficial portion of the substantia propria.

¹ It is to be remembered that the scleral ossicles of Sauropsida are homologous not with the scleral ossicles of fishes, but with the circumorbital bones. The ossicles of the sturgeon are derived not from the sclera but from the skin (H. Müller, 1872), p. 317.

*Xiphias**Thunnus*

Minnow

(2) An intermediate layer between the dermal and scleral portions corresponding topographically to the episcleral tissue. It consists of very loose lamellar tissue, so loose that it readily allows the superficial layer to be peeled from the deeper and occasionally permits some degree of movement of the globe under the dermal cornea (the eel, *Anguilla*) (Hein, 1913). It is interesting that on luxation of the eye the scleral cornea readily splits from the dermal so that the latter may remain in place and be left behind (Rochon-Duvigneaud, 1916) (cf. Fig. 324).

(3) A scleral layer consisting of dense lamellæ of substantia propria structurally continuous with the sclera itself.

(4) Descemet's membrane and its endothelium of extreme delicacy. In some species, indeed, the endothelium and Descemet's membrane appear to be absent in the central area of the cornea (carp, *Cyprinus*—Smelser and Chen, 1954) (Fig. 325).

So far this arrangement somewhat resembles that seen in lampreys,¹ and appears to be more primitive than the typically vertebrate selachian cornea. In some species, however, there is an apparently separate layer of coarse fibres on the inner aspect of the finely lamellar scleral layer—the AUTOCHTHONOUS LAYER of Leuckart (1876). It thickens greatly towards the periphery and terminates abruptly at the scleral margin, but is probably merely a modified portion of the scleral cornea.

An interesting phenomenon is the occurrence of yellow pigmentation in the corneæ of many Fishes due to the presence of xanthophores in the epithelium. In the bull-head, *Cottus*, for example, there is a pigmented process running over the cornea like a yellow waterfall (Walls and Judd, 1933), while the entire cornea of the carp, *Cyprinus*, and the pike, *Esox* (Schiefferdecker, 1887) is yellow. It is interesting that Soemmerring (1818) in describing this appearance originally, attributed it to a yellow aqueous humour. The pigment must act as a light-filter as does yellow pigmentation in the lens.²

A regular feature of the teleost cornea is an accumulation of cells, apparently continuous with the endothelium, which fills the angle of the anterior chamber and is reflected over the surface of the iris to form a massive ANNULAR LIGAMENT (Angelucci, 1881; Lauber, 1901), the "vesiculo-hyaline tissue of the angle" of Rochon-Duvigneaud (1943) (Fig. 326); from it the tensor choroideæ muscle is probably derived. The annular ligament, somewhat reminiscent of the endothelial proliferation seen in Cyclostomes and Chondrosteans, is elaborately developed in Teleosteans. It is composed of large polyhedral epithelioid cells (Giacomelli, 1935); it may be vascularized (the mud-skipper, *Periophthalmus*³) or contain melanophores (the cod, *Gadus*) and is sometimes rich in lymphatic sinuses which, however, cannot be considered homologous with the canal of Schlemm (Franz, 1910;

¹ p. 265.

² Compare the yellow pigmentation in the cornea of the bow-fin, *Amia*, in the lenses of the lamprey and of diurnal snakes and squirrels, or yellow oil-globules in some retinal cones (p. 656).

³ p. 326, Fig. 386.

Karsten, 1923). Not only does this layer cover most of the anterior surface of the iris, but in a few Teleosteans it appears to form a thick stratum, in part fibrillar, in part cellular, on the inner aspect of the scleral cornea—the SUPPLEMENTARY LAYER of Rochon-Duvigneaud

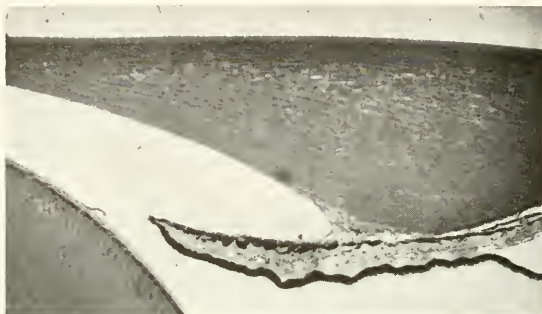


FIG. 326.—THE ANGLE OF THE ANTERIOR CHAMBER OF THE TROUT.

Showing the immense thickening in the periphery of the cornea and the annular ligament filling up the angle of the anterior chamber and binding the iris to the cornea. The dermal layer of the cornea (as often occurs) has been lost ($\times 84$) (Norman Ashton).



Gobioides

(1943) (goby-fishes, *Gobioides niger*, *Periophthalmus*; the soles, Soleidae, etc.). Various views have been put forward as to the nature of this structure which may add another layer to the already complex cornea and appears topographically to be continuous with the choroid; a

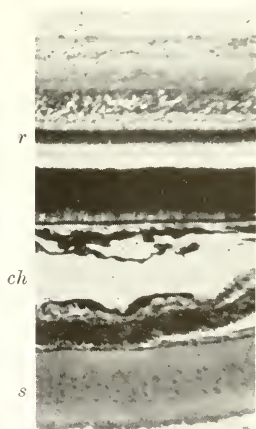


FIG. 327.—SECTION THROUGH THE EQUATORIAL SEGMENT OF THE EYE OF THE TROUT.

Showing the thick choroid, *ch*, the retina, *r*, and the scleral cartilage, *s* (Feulgen; $\times 60$) (Katharine Tansley).

secretory function has been suggested, but its exact significance must await further study (see Ballowitz, 1913; Kolmer, 1913; Remotti, 1929; Schaffer, 1929; Baecker, 1931).

The *uveal tract* shows several distinctive characteristics (Fig. 327). The choroid has the essential vertebrate structure of a chorio-capillaris and a heavily pigmented vascular layer, but is noteworthy for three features—the argentea, the choroidal gland and the falciform process. In the majority of pelagic forms there is a layer of guanine-laden cells interspersed with chromatophores—the ARGENTEA—jacketing the outside of the choroid with a silvery coat which is continued forwards over the anterior surface of the iris giving it its metallic appearance. In view of the fact that it is obscured from the retina by pigment, this layer can have no visual value;

FIGS. 328 AND 329.—THE CHOROIDAL GLAND OF THE TROUT, *SALMO TRUTTA*
(Norman Ashton).

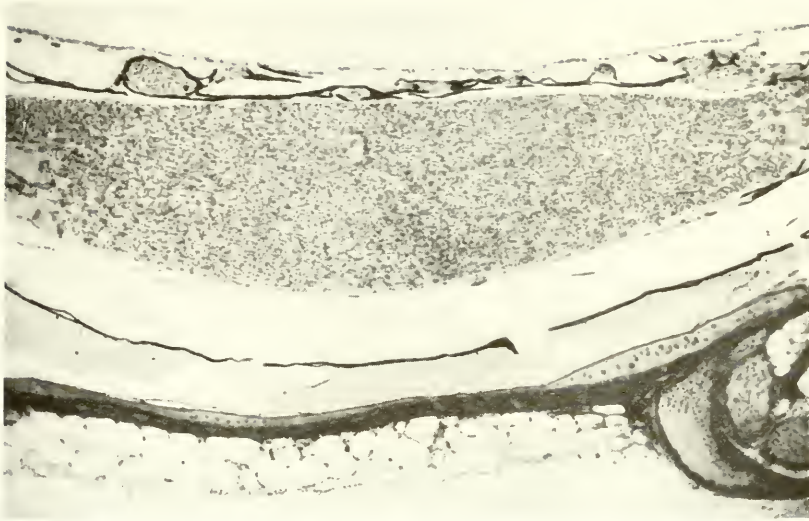


FIG. 328.—The "gland" occupies the upper part of the figure ($\times 80$).

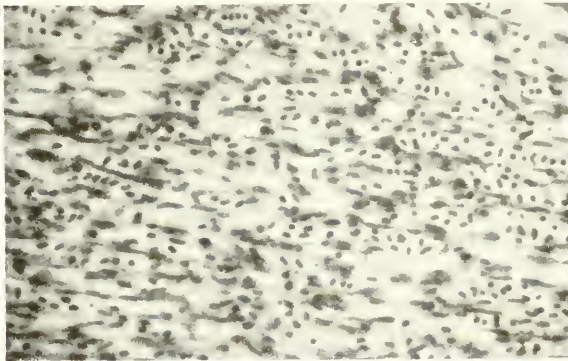


FIG. 329.—Structure of the "gland" ($\times 320$).

it is possible that it serves a protective disguise in the transparent larva the black eyeball of which would otherwise be dangerously conspicuous, blending with the reflexes of the water in the same way as do the silver reflections from the sides of the adult fish. In a few species there is, in addition, a *TAPETUM FIBROSUM* on the inner aspect of the choroid separating the main vascular layer from the choriocapillaris, such as is typical of hoofed Mammals (Milot, 1923)¹; it is composed of a layer of dense fibrous tissue of a glistening tendon-like structure wherein the

¹ p. 457.

THE EYE IN EVOLUTION

FIGS. 330 AND 331.—THE FALCIFORM PROCESS, IN AN ADULT TELEOSTEAN (TROUT).

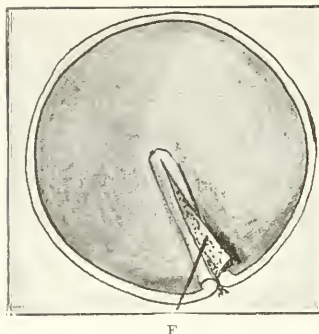


FIG. 330.—The macroscopic intra-ocular appearance of the posterior half of the globe seen from the front. F, falciform process.

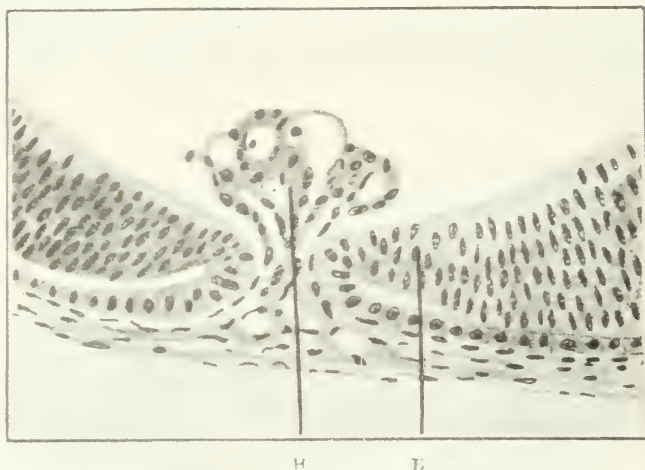


FIG. 331.—Section across the region of the fetal fissure. H, vascular mesoderm of the falciform process; E, neuro-ectoderm of the wall of the optic cup (Mann, after von Szily).

other choroidal constituents (pigment cells and vessels) have been cut down to a minimum (Walls, 1942).

The CHOROIDAL GLAND, an organ so called by Cuvier (1805) but with no structural or functional affinities to a gland, is a peculiar vascular formation lying in the posterior part of the globe between the choroid and the sclera (Figs. 328-9). It is highly vascularized, consisting essentially of a mass of juxta-apposed capillaries sometimes forming a ring around the optic nerve, more frequently horse-shoe-shaped in which case the open end of the horse-shoe, ventral to the nerve, may

be partially filled by a similar accessory body, the LENTIFORM BODY. It occurs in the majority of Teleosteans (Erdl, 1839)—according to J. Müller (1840), in all those provided with the hyoid gill (or pseudobranch) from which it is directly supplied with highly oxygenated arterial blood; from the "gland" the blood flows into the choroidal circulation. Both the pseudobranch and the choroidal gland are absent in some genera with small eyes, such as the eels (*Anguilla*) and the cat-fishes (Siluroids).

It has been suggested that the choroidal gland forms a special mechanism whereby the circulation is maintained despite considerable changes in pressure when rapid alterations occur in the depth of swimming (Allen, 1949); this, however, seems unlikely in view of its constant presence whatever the habitat of the fish. Nor does it appear to act as an erectile organ assisting accommodation by pushing the retina forwards (Barnett, 1951; Yamasaki, 1954); it is probably purely nutritive in function.

The vascularisation of the inner eye is further maintained by the falciform process, or when it is absent, by a hyaloid system of vessels. The FALCIFORM PROCESS is a peculiarity of Teleosteans and consists of a prominent sickle-shaped ridge of pigmented and richly vascularized choroidal tissue which protrudes through the inferior part of the retina in the region of the foetal fissure (which has never closed), running from the optic disc to the ciliary region (Figs. 330-1) (Franz, 1910). This structure is somewhat analogous to the cone of Reptiles and the pecten of Birds although these structures are ectodermal in origin and are secondarily vascularized. In some species the fissure has closed posteriorly so that only the anterior portion of the falciform process remains (the cod, *Gadus*; herring, *Clupea*; carp, *Cyprinus*; etc.). In those species in which the process is small or absent, as in certain eels (conger, H. Virchow, 1882), cyprinoids such as the carp and roach (O. Schultze, 1892), and goby fishes (Karsten, 1923), the nutriment of the inner eye is taken over by a hyaloid system of vessels which, like the falciform process, issues through the foetal fissure: the main artery enters the eye in the region of the optic disc and instead of running through the choroid to constitute the basis of the falciform process, breaks into the superficial layers of the vitreous and forms a dense vascular plexus running anteriorly lying loosely upon the inner surface of the retina (Chrustschoff, 1926) (Figs. 332-3). This MEMBRANA VASCULOSA RETINÆ constitutes an arrangement of widespread distribution among Vertebrates and is comparable to that seen in certain Amphibians and Reptiles (snakes). It is to be noted that these vessels ramify in the vitreous, lying superficially on the retina without entering it. The veins drain anteriorly into an annular vein which leaves the eye through the ciliary zone, and between the two a widely-

*Anguilla*

Cat-fish

*Gadus**Clupea harengus*

meshed net is spread in which the capillaries are associated with the veins leaving a zone free of small vessels around the arteries.

An exception of more than usual interest is seen in the eel, *Anguilla*. This fish is unique in having no demonstrable choroid, for the large cells of the retinal pigment epithelium lie directly on the sclera, and as if in compensation the vessels of the membrana vasculosa vascularize the retina directly (Fig. 334) (W. Krause, 1876; Virchow, 1882; Denissenko, 1882; Michaelson, 1954). The vessels of this membrane

FIGS. 332 AND 333.—THE MEMBRANA VASCULOSA RETINÆ OF TELEOSTEANS.

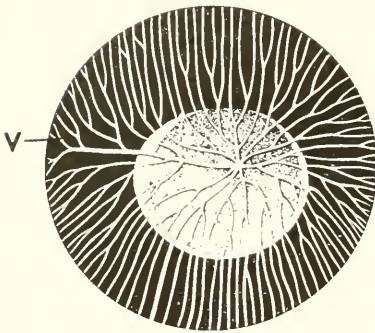


FIG. 332.—In the goby fish, *Gobius pacilichthys*. The vessels emanate from the central artery of the retina and run over this tissue within the vitreous. The division of the principal vessel into the annular vein is seen on the nasal side, at V (after Karsten).



FIG. 333.—Sketch of injected retina of the roach, *Rutilus*, showing the concentration of capillaries around the vein (to the left) while the peri-arterial zone (to the right) is relatively free from capillaries ($\times 23$) (I. C. Michaelson).

derive from a large central artery entering the eye, as is usual, through the optic disc and its branches form an arterial network in the vitreous lying on the surface of the retina and extending to the periphery of the fundus where they form capillary loops. From this arterial network numerous branches pass from the vitreous through the internal limiting membrane into the retina: Virchow (1882) estimated that there were 9,600 of them. In the substance of the retina they divide into two strata of capillaries, one in the inner and one in the outer nuclear layer, and from these retinal capillary nets blood is drained by large veins which combine to form four main vessels and eventually join to form a central vein in the optic nerve head (Figs. 334 and 335). The absence of a choroid in this fish is unique and the direct vascularization of the inner retinal layers constitutes the only known exception

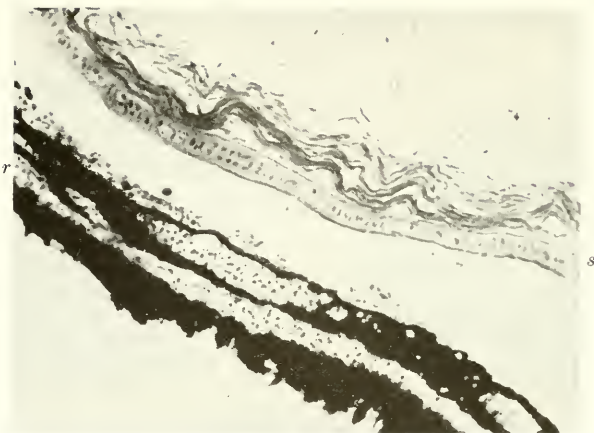


FIG. 334.—SECTION OF THE EYE OF THE EEL.

The superficial vitreous and both retinal capillary nets can be seen filled with indian ink (*r*). The cells of the retinal epithelium form a broad layer. There is no choroid present, the epithelial layer lying directly on the cartilaginous sclera (*s*) ($\times 169$) (I. C. Michaelson).



FIG. 335.—THE RETINA OF THE EEL.

Injected with indian ink, mounted in glycerine. The superficial vitreous vessels are in focus: these are arterial ($\times 37$) (I. C. Michaelson).

to the general avascularity of the teleostean retina; indeed, it is the only known case in which the vertebrate retina is directly vascularized except in the colubrid snake *Tarbophis* and in Mammals.

The *ciliary zone* is narrow and, without folds or processes, may be said not to exist so that the choroid appears to pass directly into the iris (Fig. 336)¹; only in a few amphibious types such as *Anableps* do a few processes exist. This region, however, provides the supporting and accommodative apparatus of the lens. Dorso-nasally the latter

¹ See footnote p. 267.

is suspended pendulum-like by a firm suspensory ligament, a condensation of the anterior vitreous with a fibrillar appearance on microscopic examination (Harms, 1928 ; Teulières and Beauvieux, 1931 ; Koch, 1952). Ventrally, at the ciliary end of the falciform process, a small structure of great variability in size and shape makes contact with the lens by ligamentous condensations of the vitreous—the CAMPANULA of Haller (1762). It contains a triangular muscle of smooth fibres of ectodermal origin being derived from the retinal epithelium of the ciliary zone at the open lips of the foetal fissure, thus resembling in this respect the muscles of the iris (Nussbaum, 1901 ; v. Szily, 1922), and is innervated by a short ciliary nerve from the



FIG. 336.—THE ANTERIOR SEGMENT OF THE EYE OF THE BULL-HEAD, *COTTUS BUBALIS*.

i, iris ; *sl*, suspensory ligament ; *s*, serous spaces behind the annular ligament ; *ca*, scleral cartilage ; *co*, conjunctiva ; *c*, cornea ; *p*, posterior layer of the cornea ; CH, campanula of Haller (after a drawing by Rochon-Duvigneaud).

ciliary ganglion (Tretjakoff, 1926 ; Meader, 1936). It has been generally accepted as being the effector muscle in the accommodative mechanism, acting by retracting the lens towards the retina, a claim, however, contested by Bourguignon and Verrier (1930) who failed to find muscular tissue in this somewhat peculiar structure. Whatever its true nature, it is a characteristic of Teleosteans, being absent only in a few species such as the eel.

An additional muscle is found in this region in practically all species—the TENSOR CHOROIDEÆ. It was initially described as being composed of fibrous tissue and named the " ciliary ligament " (Leydig, 1853 ; Leuckart, 1876), but has been shown to contain smooth muscle fibres (Grynfeldt, 1910 ; Rochon-Duvigneaud, 1943). It is a tenuous muscle, about 1.5 mm. in length, lying between the sclera and the uvea, arising from the annular ligament anteriorly, thus anchoring itself to the cornea, and inserting itself into the anterior part of the choroid just behind the ora (Faravelli, 1890–91 ; Grynfeldt, 1910 ; in the scorpion-fish, *Scorpena*, there is an additional slip



Scorpena

PLATE II
THE IRIDES OF TELEOSTS (Ida Mann)

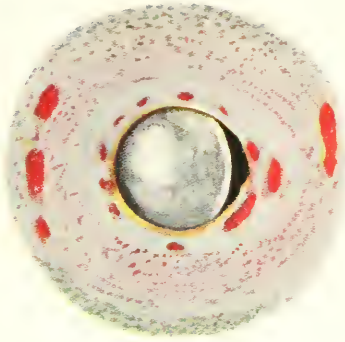


FIG. 1.—The kullfish, *Aplocheilichthys rubrostigma*.

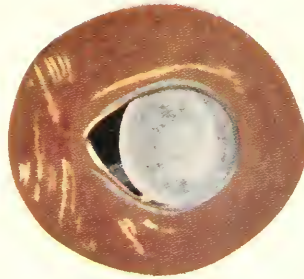


FIG. 2.—The salmon, *Salmo salar*.

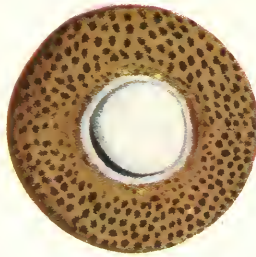


FIG. 3.—The telescope-eyed goldfish, *Carassius*.

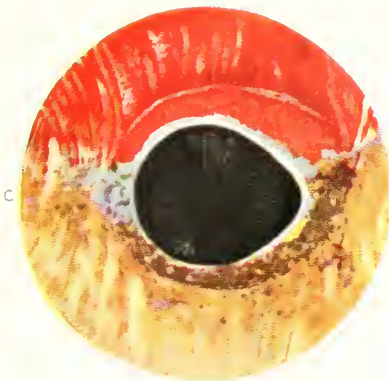


FIG. 4.—The red-eyed fish, *Tetraodonopterus rubropictus*.
C, ciliary arteries.



FIG. 5.—The common goldfish, *Carassius auratus*.
C, ciliary arteries.

running between the cornea and the sclera, while in *Beryx* the entire muscle seems to pass from the cornea to the sclera without a choroidal attachment (Rochon-Duvigneaud, 1943).

The tensor choroideæ is generally accepted as the precursor of the ciliary muscle (of Brücke) of Sauropsida and Mammals, but in Fishes its function is not clear; it has been said to brace the retina and choroid when the lens presses backwards upon the vitreous during accommodation (Beer, 1894), while the main role in teleostean accommodation was ascribed to it by Bourguignon and Verrier (1930).¹



Beryx

The *iris* is complex in structure and frequently brilliantly coloured. The continuation of the choroidal argentea over its anterior surface gives it a metallic sheen and in addition bright pigments abound—gold, scarlet, yellow, mauve and others, sometimes so dense that the structure of the tissue or the arrangement of its vessels is completely obscured (Plate II). In some species Beer (1894) found that a slow change in colour could be induced by electrical stimulation, presumably owing to contraction of the chromatophores; a similar change has been induced in the carp, *Cyprinus*, by the injection of adrenalin or ablation of the hypophysis (Rochon-Duvigneaud, 1943). The two ectodermal layers conform to the usual pattern, the posterior being non-pigmented almost half-way towards the pupil, the anterior heavily pigmented throughout its extent. From the latter are developed the myoepithelial fibres of the sphincter muscle; in most species a few radial cells represent the elements of a dilatator muscle although in some these may be marked (the sword-fish, *Xiphias*—Barraquer-Cerero, 1952). Anterior to the ectodermal layer the heavily pigmented vascular layer forms the forward continuation of the choroid, covered superficially by the thick argentea; while over a varying portion of the peripheral area of the anterior surface of the iris the cellular annular ligament spreads itself, filling up the angle of the anterior chamber in continuity with its corneal extension. The iris is usually supplied by two anterior ciliary arteries which enter in the horizontal meridian on either side and run on the superficial surface straight towards the pupil: here they divide to form a circular arterial anastomosis around the pupillary margin (Plate II, Fig. 5). The venous drainage is by deeper vessels running beneath the argentea, and therefore hidden from view; they are continuous with the choroidal veins (J. Müller, 1840; Virchow, 1882; Mann, 1929–31).



Xiphias

The *pupil* is round or horizontally oval or pear-shaped, but in general, even in the rare types wherein the sphincter forms a massive band, the pupils of Teleosts are essentially immobile, the iris being widely fixed to the posterior surface of the cornea by the annular ligament. As with selachian irides, the pupils contract sluggishly and

¹ p. 646.

autonomously by the direct action of light (Brown-Séquard, 1847-59 ; Magnus, 1899) (Figs. 337-9).

Only in a few species, such as the flounders with upward-looking eyes, and the eels, does much pupillary excursion occur ; in the pearl-fish, *Encheliophis*, also with upward-looking eyes, the pupil is highly contractile. Some cat-fishes have an operculum which reduces the pupillary aperture to a circular slit

FIGS. 337 TO 341.—THE PUPILS OF TELEOSTEANS.



FIG. 337.—The Moray eel, *Gymnothorax*.



FIG. 338.—The sailfish, *Istiophorus*.



FIG. 339.—The flounder, *Pleuronectes*.



FIG. 340.—The serpent eel, *Leptognathus*.



FIG. 341.—The cat-fish, *Plecostomus*, showing the operculum in various stages of closure of the pupil.

(*Plecostomus*, Fig. 341), while the serpent-eel of New Zealand (*Leptognathus*) has a secondary pupillary aperture in its lower part giving it a double effect (Fig. 340).¹ An interesting feature is the common presence of an aphakic area in the pupillary aperture which the lens rarely entirely fills (Plate II). This is sometimes situated below but is usually on the temporal or nasal side and becomes particularly marked when the lens is drawn sideways in accommodation (Beer, 1894).

The *lens* of Teleosteans is usually spherical, approximating the cornea, with a large spherical nucleus and a well-marked system of sutures usually taking the form of a single line as in Selachians but sometimes star-shaped (Figs. 314, 342) (Rabl, 1898 ; Koch, 1950-52) ; Yamasaki, 1953). The peripheral shell has a refractive index approximating that of water ; the central core, on the other hand, has the high refractive index of 1.5 and is the effective refractive constituent of the optical system (Hogben and Landgrebe, 1940). The vitreous is dense and filamentous (Koch, 1952-53).

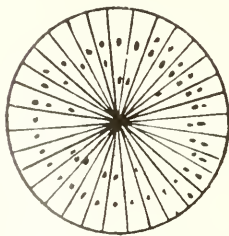


FIG. 342. — LENTICULAR SUTURES OF TELEOSTS.

The usual system is that of Selachians (Fig. 314) ; * star-shaped system is also relatively common.

The teleostean *retina* is an advanced and fully differentiated structure with, as we have already seen, an open foetal fissure, nourished

¹ p. 325.

(with the exception of the eel) either by the falciform process or a hyaloid system of vessels. The pigmentary epithelium has a normal configuration (Fig. 343), but in some species (Cyprinidae, Percidae) has an ocellus-like RETINAL TAPETUM LUCIDUM of varying extent, sometimes small, sometimes occupying a large oval area or almost the entire fundus. In the region thus occupied the epithelial cells have long processes heavily packed with crystals of guanine or a guanine-like compound containing calcium; in dim light the fuscine pigment migrates backwards into the cell-bodies exposing a silvery mirror of guanine; in bright light the dark pigment migrates through the guanine layer to the tips of the processes, covering up the tapetum and absorbing the excess of incident light (Schiefferdecker, 1887; Abelsdorff, 1896; Gatten, 1907; Wunder, 1925-30). Occasionally in abyssal fishes which are never exposed to bright light (*Evermannella*), the pigment does not migrate and is confined to small masses at the ends of the cell processes, an arrangement also seen in Chondrosteans.

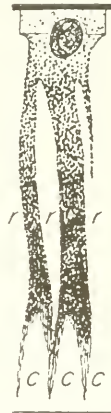


FIG. 343. — THE PIGMENT EPITHELIUM OF THE GOLD FISH, *CARASSIUS AURATUS*.

In the light-adapted state. The processes contain migratory pigment in rod-like granules concentrated mainly in their tips. *r* and *c* represent spaces occupied by rods and cones (after Walls).

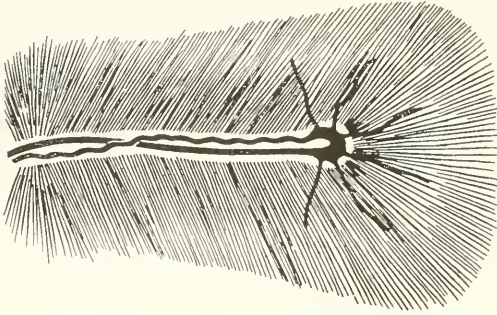
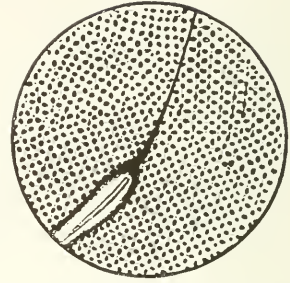
The visual retina has received much study (Figs. 344-6).¹ This structure in Teleosts is remarkable among Fishes for the regularity of its layers and the absence of displaced elements, the thickness of the nuclear layers and the number of ganglion cells; it is the most highly differentiated retina among the Fishes and compares in this respect only with the highest Vertebrates. Typically both rods and cones are found: only rarely as in deep-sea species (*Bathytroctes*) and exceptionally in fresh-water types (*Hiodon*) are the cones absent (Moore, 1944). In deep-sea forms, in order to increase the sensitivity to light, the rod population is usually dense and may indeed be the highest among all Vertebrates (5,000,000 sq. mm. in *Lampanyctus*—Vilter, 1951) (Wunder, 1925-30) while the individual elements may be elongated; in a bathypelagic species, *Bathylagus benedicti*, they are arranged in three distinct rows (Vilter, 1953).

Presumably as an adaptation to increase the visual acuity in the direction in which food is usually obtained, different areas of the retina frequently vary in the relative density of the population of rods and cones; thus in the minnow, *Ercymba*, which frequents the bottom, the ventral area of the retina contains

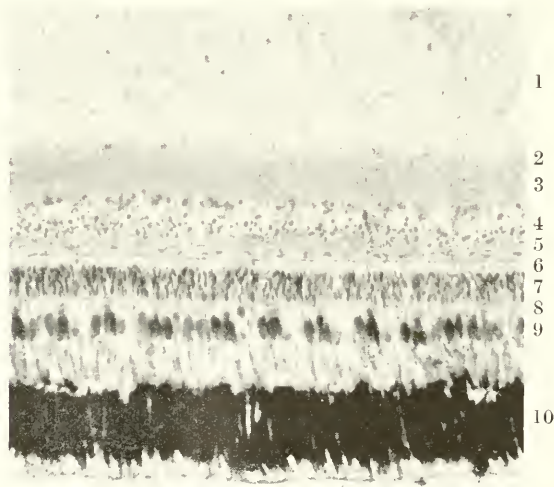
¹ H. Müller (1857), M. Schultze (1866), Dobrowolsky (1871), W. Müller (1875), Hannover (1876), Denissenko (1881), W. Krause (1886), Cajal (1893-1933), Greeff (1899), Hesse (1904), Wunder (1925-30), Arey (1928), Verrier (1928-38), Mayou (1933), Rochon-Duvigneaud (1943), Vilter (1947-54), Sverdlück (1954), H. Müller (1954).

THE EYE IN EVOLUTION

FIGS. 344 AND 345.—THE OPHTHALMOSCOPIC APPEARANCE OF THE FUNDUS OF TELEOSTEAN FISHES.

FIG. 344.—The cod, *Gadus*, showing the vessels of the falciform process running over the elongated optic disc and breaking up into 6 branches of the hyaloid artery (after Beauregard).FIG. 345.—The scorpion fish, *Scorpaena*, showing the optic nerve entrance in relation to the falciform process and the peculiar mosaic arrangement of the background of the fundus (after Franz).

These illustrations may seem to require an apology but the fundus of a fish is very difficult to see ophthalmoscopically. It can be examined out of water if the fish be kept alive by a current of water supplied to the mouth and gills; some species such as the carp can survive being kept out of water for some time. The difficulties do not end here. Out of water the cornea is irregular; and in addition to the great hypermetropia in air of an eye optically designed for vision under water, the spherical shape of the crystalline lens makes the dioptries such that only a minute portion of the fundus can be seen at one time and no overall view can be obtained.

FIG. 346.—THE RETINA OF THE TROUT, *SALMO TRUTTA*.

1, optic nerve fibre layer; 2, ganglion cell layer; 3, inner plexiform layer; 4, inner nuclear layer with a prominent layer of large horizontal cells (5); 6, outer plexiform layer; 7, outer nuclear layer; 8, external limiting membrane; 9, visual cells; 10, rods ensheathed in pigment (light-adapt) (Azan; $\times 112$) (Katharine Tansley).

40% more rods than the dorsal area (Moore *et al.*, 1950), in the pelagic dragonet, *Callionymus*, the dorsal half is almost entirely populated by cones, the ventral by rods (Vilter, 1947), while in the sardine, *Clupea pilchardus*, which feeds on Crustaceans in the water above it, this relationship is reversed (Vilter, 1950). This adaptation may develop with the growth of the fish and a change in its habitat; thus in the elver (and cavernicolous eels) the rods are more numerous in the ventral part of the retina, while in adult eels in rivers they are more numerous in the dorsal area (Vilter, 1951).

The rods are usually small, elongated and very numerous, although in some species (the cat-fish, *Ameiurus*) they are thick, plump and few in number (18,400/sq. mm.). The cones, in contradistinction to the rods,



Ameiurus

FIGS. 347 TO 349.—THE VISUAL CELLS OF TELEOSTS ($\times 1,000$)
(Gordon Walls).

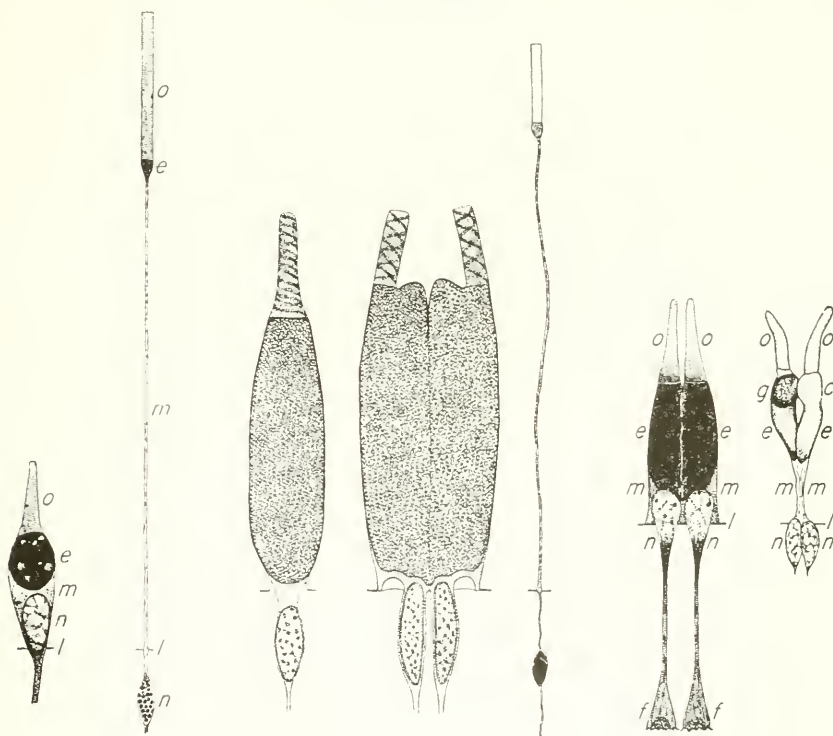


FIG. 347.

FIG. 348.

FIG. 349.

FIG. 347.—The cone and rod of the goldfish, *Carassius*.

FIG. 348.—A single cone, a twin cone and a rod of the pike-perch, *Stizostedion*.

FIG. 349.—The twin cone of the sunfish, *Lepomis* (light-adapted) and the conjugate element of *Fundulus* (after Butcher, 1938).

c, "clear mass" and g, "granular mass" in the conjugate element;
e, ellipsoid; f, footpiece; l, external limiting membrane; m, myoid;
n, nucleus; o, outer segment.

*Fundulus*

are relatively bulky (Fig. 347). These are remarkable for the presence of twin and double cones. DOUBLE CONES, seen also in Holosteans and widely distributed among most Vertebrates, occur in many Teleosteans such as the roach, *Rutilus* (Greeff, 1899), the goldfish (Walls, 1942), some of the Salmonidæ (Verrier, 1935; McEwan, 1938), the killifish, *Fundulus*, and others. They were first described by Hannover (1840), M. Schultze (1867) and Dobrowolsky (1871) and consist of the fusion of two dissimilar cones in the lower myoid region, one, a large cone, being the chief element and the only one which participates in photo-mechanical movements, the other, a smaller accessory element with an unusually large parabolid. There are two nuclei, and the two foot-pieces may connect with different bipolar cells. TWIN CONES, on the

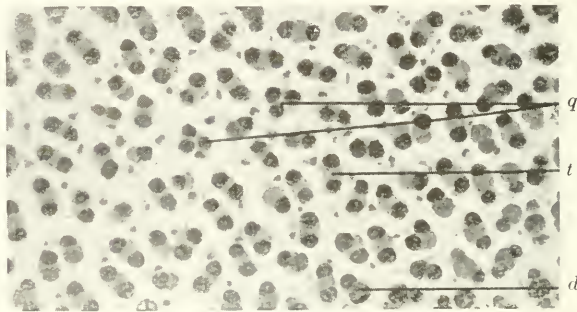


FIG. 350.—TRIPLE AND QUADRUPLE CONES IN A TELEOSTEAN FISH.

A tangential section through the retina of the minnow, *Phoxinus phoxinus*, to show double, *d*, triple, *t*, and quadruple, *q*, cones ($\times 500$) (A. H. Lyall).

other hand, are found only in the teleostean retina in which their occurrence is widespread (Fig. 348-9). In these the two elements, fused throughout their entire inner segments, are identical and both contract and elongate in photomechanical movements. Twin cones are more numerous in the central retina than the peripheral and in surface fish than deep-sea types; in some particularly active species they are the only cone elements encountered (flat-fishes; some species of scorpion-fish, *Scorpaena*; cod, *Gadus*; etc.) (Wunder, 1925-30). While they are thus associated with vision in bright light, they do not seem to subserve accuracy of vision since they are absent from the fovea when this is present.

*Salmo trutta*

MULTIPLE CONES (triple and quadruple) have been described by Lyall (1956-57)—triple cones¹ in the retina of the trout, *Salmo trutta*, which appear to be anomalous double cones; and triple and quadruple cones in the retina of the minnow, *Phoxinus*, where they occur in considerable numbers (Fig. 350). In

¹ Triple cones have also been described in the frog, *Rana temporaria* (p. 342) and the gecko, *Aristelliger* (p. 364). See, however, p. 253.

this species the triple cone consists of a large central cone with two smaller ones on either side of it; the quadruple cones are formed by three small cones grouped symmetrically around a large central cone. A physiological explanation of the significance of double, twin or multiple cones has not yet been advanced.¹

In most Teleosteans the retina shows a circumscribed region where it is thicker and more highly packed with visual elements than is the remainder of the fundus, constituting an ill-defined area centralis;

FIGS. 351 TO 353.—THE FOVEA OF TELEOSTS.

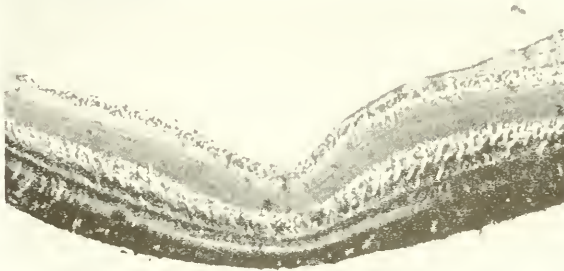


FIG. 351.—Section through the fovea of the blenny, *Blennius*.

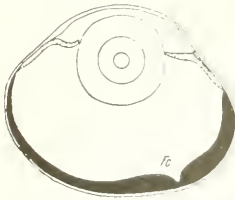


FIG. 352.—The fovea, *Fo*, of the sea-horse, *Hippocampus*.

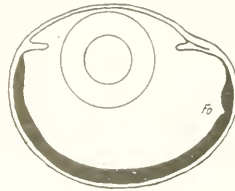


FIG. 353.—The fovea, *Fo*, of the sea-bass, *Serranus* (Kahmann, v. Graefes *Arch. Ophthalm.*).

here the density of the cones, the bipolar cells and the ganglion cells is increased. In the guppy, *Lebistes*, and the killifish, *Fundulus*, the area is apparently duplicated, one lying axially, another ventrally (Vilter, 1948). In a number of species, particularly the agile and lively inhabitants of the littoral zone, a fovea is present in addition in the horizontal meridian of the temporal retina (Kahmann, 1934–36) (Figs. 351–3). Among Fishes this is unique to Teleosteans. It usually takes the form of a shallow pit, inferior in its retinal differentiation to the corresponding area in lizards, Birds and Primates, but it may be well formed (pipe-fish, *Syngnathus*—Krause, 1886; the labrid, *Julis*, and the blenny,



Syngnathus

¹ p. 253.

*Blennius**Bathylagus*

Blennius—Verrier, 1933) and on occasion is deep and highly organized, as in the sea-bream, *Girella* (Verrier, 1935).¹ With few exceptions such as the sea-horse, *Hippocampus*, where it is nearly central (J. Carrière, 1885), it is typically situated temporally in the region of the retina which could be used for binocular vision. In this region rods and twin cones are excluded and the single cones are densely packed, long and rod-like, while the other retinal layers, including the ganglion cells, become attenuated but do not disappear. It is interesting that in some deep-sea Teleosts (*Bathytroctes*, *Bathylagus*) with a pure-rod retina, the rare occurrence of a temporal fovea populated with rods is found (Brauer, 1908)²; in *Bathylagus* there are 6 superimposed rows of rods in this region instead of the usual 3 found elsewhere in the retina

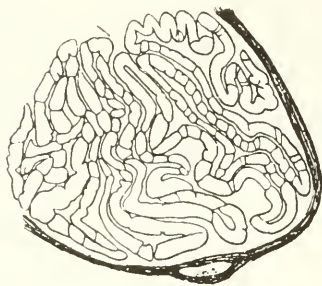


FIG. 354.—THE OPTIC NERVE OF TELEOSTS.

Cross-section of the optic nerve of *Serranus cabrilla* showing the folded ribbon structure (after Studnicka).

(Vilter, 1954), an arrangement which may act by increasing the sensitivity to light.

The optic nerve, even in Teleosteans, is relatively primitive (Ucke, 1891; Deyl, 1895; Lumbroso, 1935). In many species the disc is narrow and oblong, for the nerve fibres leave the retina not only at this point but for some distance along the open foetal fissure. The nerve thus emerges from the eye as a tape rather than a cord assuming a circular cross-section in the orbit, and on section the nerve fibres appear as a broad pleated ribbon folded concertina-like to accommodate itself into its tubular sheath (Fig. 354). In a few species on approaching the globe the nerve divides into as many as a dozen strands so that it enters the eye in multiple rootlets with a corresponding number of optic discs (the bull-head catfish, *Ameiurus*, the loach, *Misgurnus*, and the deep-sea *Polyipnus*).³ A septal system may be absent or represented

*Hippocampus**Misgurnus*

¹ Other foveate Teleosts are the butter-fish, *Pholis*, the puffer-fish, *Tetraodon*, the sea-bass, *Serranus*, the trigger-fish, *Balistes*, and the weever, *Trachinus*.

² See, also, pp. 365, 382, 486.

³ This peculiar arrangement is also seen in *Polypterus*, some salamanders and some members of the deer family.

by a few large septa (the sword-fish, *Xiphias*, the eel, *Anguilla*), but as a general rule the simple ependymal core of the Cyclostomes has developed into a more mature system wherein the oligodendroglial cells are scattered in a nerve which is not sharply fasciculated (Prince, 1955). At the chiasma a total decussation of the nerve fibres occurs, sometimes as a simple crossing of two intact nerves, occasionally (as in the herring) one nerve button-holing through the other, or crossing in the form of interlacing bundles (Hannover, 1852 ; Parker, 1904 ; Mayhoff, 1912 ; Verrier, 1930) (Figs. 355 to 357).

It is interesting that Rasquin (1949) reported re-myelination of the optic nerve and the return of vision 4 weeks after section of the optic nerve in *Astyanax mexicanus*, provided the cut ends of the optic nerve were approximated.

FIGS. 355 TO 357.—THE CHIASMA OF TELEOSTS.

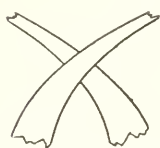


FIG. 355.—The usual configuration: the simple crossing of intact nerves.

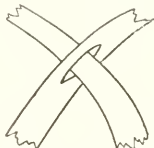


FIG. 356.—The herring: the button-holing of one nerve by another.

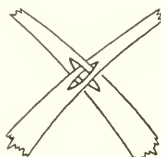


FIG. 357.—The parrot-fish: the interlacing of bundles.

THE OCULAR ADNEXA. The eyeball is marked off from the surface of the head by a **CIRCUMOCULAR SULCUS**, a shallow depression between the corneal epithelium and the skin running circumferentially around the globe ; this represents the conjunctival sac and affords the globe the small liberty of movement it possesses. The outer margin of this sulcus constitutes a poorly developed **LID-FOLD**—the only representative of eyelids. Such a rudimentary arrangement is in marked contrast to the relatively well-formed lids in Selachians.¹ In a number of swift-swimming pelagic types, however, particularly the herrings (*Clupeidæ*) and the mackerels (*Scombridæ*), the eye is partially covered by **ADIPOSE LIDS**, thin cutaneous folds often enclosing fatty tissue arising from the outer lip of the circumocular sulcus. They are usually vertically disposed, one anteriorly and one posteriorly so that when these lids are well developed the aperture is a narrow vertical ellipse, as in the skip-jack, *Pomolobus* ; occasionally they are fused so that the globe is covered except for a circular opening opposite the pupil, as in the mullet, *Mugil* ; rarely the skin-folds fuse completely across the eye (as in the anchovy, *Engraulis*, and relatives of the herring such as *Chanos*) (Hein, 1913 ; Walls, 1942). In this last event the

¹ p. 289.

fused lids become extremely thin and transparent forming a "secondary spectacle",¹ and between them and the corneal epithelium there is a closed "conjunctival sac" lined by epithelium (Fig. 279).

The Salmonidae (the salmon-trout family) have a peculiar arrangement of lids. The posterior lid is of the usual type but the anterior, which has been called a *false nictitating membrane*, is not derived from the skin of the circum-ocular sulcus but is represented by a broad triangular fold arising deeply from the anterior rim of the membranous orbit.

The *orbit* is bony and completely enclosed; its roomy cavity is filled with loose tissue and venous sinuses serving as a cushion for the globe, which is sometimes anchored by a TENACULAR LIGAMENT. The extra-ocular muscles correspond with those of Selachians and are carried through canals in the orbital bones where they find insertion, an anterior canal serving the obliques, a posterior the recti (Corning, 1900; Allis, 1922) (Fig. 293).

THE DIPNOAN EYE

THE DIPNOI (LUNG- OR MUD-FISHES) are a very primitive stock with three surviving representatives—*Protopterus*, the African lung-fish which burrows in the earth in the dry season, the eel-like *Lepidosiren* from the swamps of the Amazon, and the 6-foot long *Neoceratodus* from Queensland (Figs. 358–360).

FIGS. 358 TO 360.—EXTANT DIPNOAN FISH.



FIG. 358.—*Protopterus*.



FIG. 359.—*Lepidosiren*.

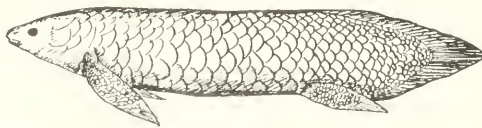


FIG. 360.—*Neoceratodus*.

The eyes of the first species have received some perfunctory study which has shown them to be very primitive structures indeed (Hosch, 1904; Grynfeldt, 1911): those of the second have been described by Rochon-Duvigneaud (1943) (Fig. 361). As in the Cyclostomes, there is a dermal cornea separate from the scleral cornea, allowing free

¹ p. 266.

rotation of the eye under the transparent skin. The thin scleral cartilage reaches only to the equator, and there is no annular ligament or meshwork in the angle of the anterior chamber, no ciliary body, zonule or muscles, and apparently no accommodative mechanism. The choroid is extremely thin and lightly pigmented without an argentea, and there is a well-developed membrana vasculosa retinae which, however, can be separated from the retina only with difficulty. The iris shows no evidence of pupillary musculature.

The retina shows several peculiarities. The cells of the pigimentary

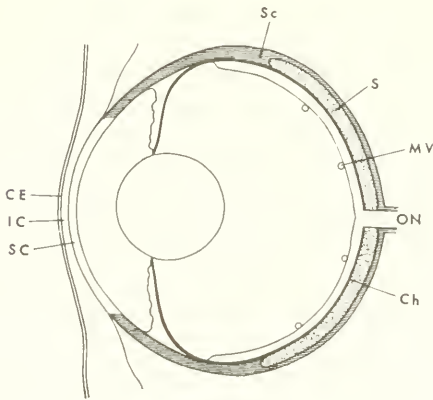


FIG. 361.



FIG. 362.

FIG. 361.—Diagram of a Dipnoan eye.

Ch, choroid; CE, corneal epithelium; IC, intermediate corneal tissue; MV, membrana vasculosa retinae; ON, optic nerve; S, scleral cartilage; Sc, sclera; SC, scleral cornea.

FIG. 362.—The pupil of *Neoceratodus*.

epithelium are enormously large so that this layer is thicker than the entire choroid and they are provided with numerous long filamentary processes (Fig. 363). In the visual retina the outer nuclear layer consists of 2 rows of cells, the inner nuclear layer of 4, and there is a single row of ganglion cells. The rods are unique—enormous and cone-like with a large oil-droplet (except in *Neoceratodus*) and a paraboloid—probably representing a very primitive type, derived, according to Walls (1942), from an archaic early cone; in *Protopterus* the cones are of two forms, single and double, also provided with oil-droplets confined to one member of the double cone (Fig. 364); in *Neoceratodus* there are single cones only; and in *Lepidosiren* the cones are absent and the retina is pure-rod (with oil-droplets) (Kerr, 1902-19).

In *Protopterus* the optic nerve, as is seen in Cyclostomes, is a single cord with an endymal core; in *Lepidosiren* and *Neoceratodus*

FIGS. 363 AND 364.—THE RETINAL ELEMENTS OF *PROTOPTERUS*
(Gordon Walls).



FIG. 363.—A PIGMENT CELL.

Showing a mass of filamentous processes laden with pigment sharply differentiated from the body of the cell. *r* and *c* represent the spaces occupied by the rods and cones respectively ($\times 500$).

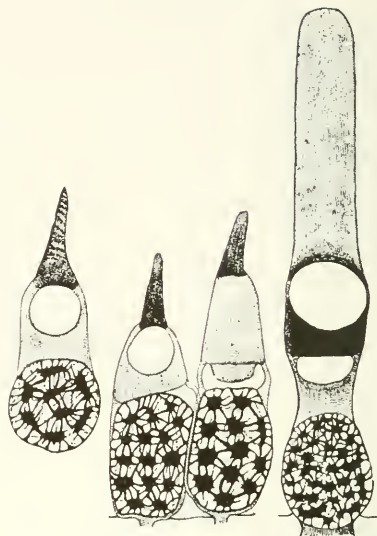


FIG. 364.—A SINGLE CONE, A DOUBLE CONE AND A ROD.

Members of the double cone are unusually loosely associated. There is an oil-droplet in the single cone and one member of the double cone. The rods are large and have an oil-droplet as well as a paraboloid ($\times 1,000$).

the nerve divides into a number of bundles each with a similar core, as if the primitive optic nerve of the lamprey had reduplicated itself several times and all the nerve-cords had been gathered in one sheath¹ (Prince, 1955).

THE COELACANTH EYE

THERE IS ONLY ONE SPECIES of this ancient order of fishes known to be extant—*Latimeria* (Fig. 365)—lately and surprisingly discovered in the Indian Ocean off the coasts of South-East Africa. The eye of this species is of great interest, showing characteristics closely resembling those of Selachians on the one hand and Chondrosteans on the other, clearly demonstrating the remarkable unity of this organ throughout the vertebrate phylum.² In general its structure shows adaptation for vision in the ocean depths where little light is available. For this reason the eye is unusually large and takes the general form of a flat-

¹ See also snakes, p. 392.

² p. 234.

tened sphere with a relatively short antero-posterior diameter (Millot and Carasso, 1955) (Figs. 366-7).

The cornea is flat and the sclera lined by a continuous cartilage, thin (0.5 mm.) in front and thick (1.8 mm.) posteriorly where it encircles the optic nerve. As with most fossil Crossopterygians and as in Chondrosteans, there is a pericorneal ring of calcified scleral plaques, 18 to 20 in number. The choroid is thin, the choriocapillaris being particularly tenuous, and there is a well-formed crystalline tapetum which, being continued over the anterior surface of the iris, gives the eye a brilliant metallic sheen. The ciliary zone is particularly rudimentary, showing no radial folds nor any structure resembling a campanula

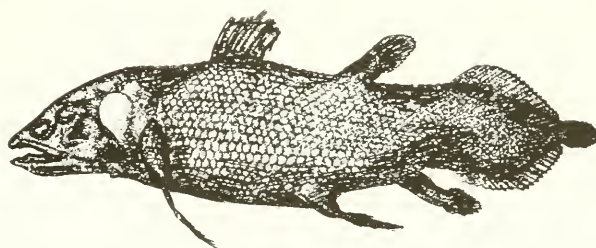


FIG. 365.—THE COELACANTH, *LATIMERIA CHALUMNAE*.
(1/16 natural size) (after Günther and Deckert).

or other focusing apparatus. The lens, which approaches the cornea leaving a very shallow anterior chamber, is almost spherical and large.

The retina is completely avascular and shows no area centralis. As would be expected in the presence of the tapetum, the epithelium is devoid of pigment. The visual cells are practically entirely represented by long, thin rods; cones are very rare and contain well-defined, colourless oil-droplets, again recalling the corresponding structures in the chondrostean eye. The general architecture of the retina is poorly differentiated although Müller's cells are particularly numerous. Ganglion cells are few and their ratio to visual elements is remarkably low. The eye is characterized by its great simplicity and primitiveness, presumably possessing a high sensitivity to light but a rudimentary visual acuity.

THE CHONDROSTEAN EYE

THE CHONDROSTEANS are represented today only by the sturgeons and the Polypterini. The sturgeons are a group of old-fashioned marine fishes which ascend rivers to shed their spawn (caviare) in the Northern hemisphere, and are today represented by *Acipenser* (Fig. 368) and a few related genera—*Polyodon*, the spoonbill sturgeon of the Mississippi, *Psephurus*, an enormous fish of the Yangtze-Kiang in China, and *Scaphirhynchus*, the shovel-nosed sturgeon of



Polyodon

THE EYE IN EVOLUTION

FIGS. 366 AND 367.—THE EYE OF THE COELACANTH (from a specimen of J. Millot, Paris).

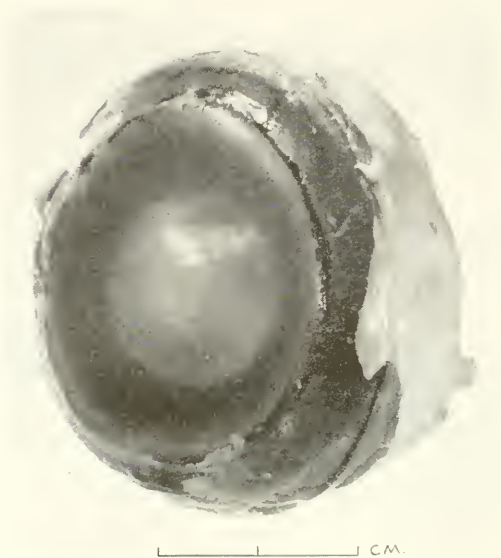


FIG. 366. The general configuration of the eye showing the short antero-posterior diameter, the large cornea through which the lens is visible, and the peri-corneal ring of calcified scleral plaques.



FIG. 367.—Section of the eye showing the large spherical lens lying close to the cornea.

North America and Asia. They are the largest fish inhabiting fresh water and are the most primitive of the bony fishes,¹ showing many selachian characteristics.

In its general shape the globe of the sturgeon is flattened as is usual in fishes (Figs. 369–70). The cornea has the standard layering and Descemet's endothelium is piled up at the angle of the anterior chamber to form an annular ligament which fills the angle with loose tissue reflected onto the iris (Baecker, 1931). The sclera is usually thick and its inner half is occupied by an immensely thick scleral cartilage which forms a feature of the eye; and in some species two crescentic bony plaques lie, one superiorly and one inferiorly, athwart the limbus



FIG. 368.—THE STERLET, *ACIPENSER RUTHENUS* (Zool. Soc., London).

external to the scleral cartilage, extending onto the cornea where they lie under the epithelium in the periphery (Soemmerring, 1818; the CONJUNCTIVAL BONE of H. Müller, 1872; Edinger, 1928).

The choroid is heavily pigmented and richly vascular, being lined externally with an argentea as in Teleosteans, while its inner $\frac{2}{5}$ just external to the choriocapillaris is occupied by a tapetum lucidum² comprised of some 12 layers of cells packed with guanine crystals interspersed with occasional pigment cells, the dense structure being pierced at intervals by vessels supplying the capillary layer for the vascular layer of the choroid (Fig. 371) (Brücke, 1845; Mürr, 1927).

The amuscular ciliary body may hardly be said to exist (Fig. 372); superiorly it gives rise to a suspensory ligament of the lens resembling that of Teleosts, and inferiorly to a papilla resembling that of Selachians which apparently does not contain muscle fibres (v. Hess, 1912). The iris also is devoid of muscles and like that of the lamprey is immobile, while the stroma contains a thick argentea, a continuation of the corresponding layer in the choroid. The immobile pupil is of the form of a vertical ellipse (*Acipenser*) (Fig. 368) or a square with rounded corners (*Scaphirhynchus*).

¹ p. 234.

² p. 609.

THE EYE IN EVOLUTION

FIGS. 369 AND 370.—THE CHONDROSTEAN EYE.

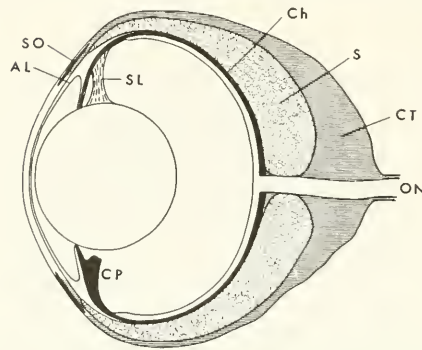
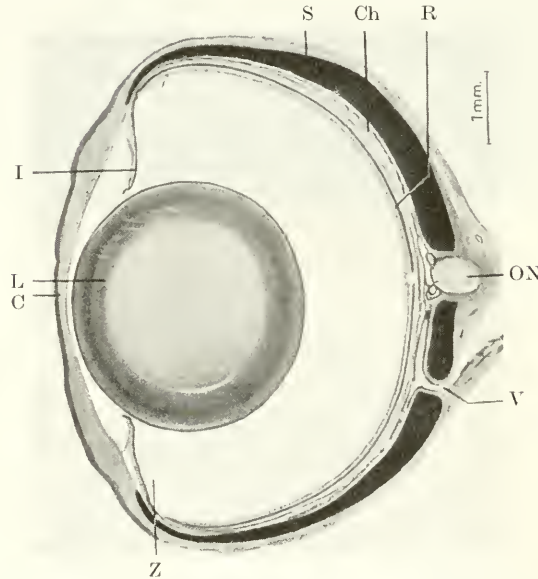


FIG. 369.—Diagram of a Chondrostean eye.

FIG. 370.—Drawing of the eye of *Acipenser ruthenus* (Rochon-Duvigneaud, *Les Yeux et la Vision des Vertébrés*; Masson et Cie).

AL, annular ligament; *C*, cornea; *Ch*, choroid; *CP*, ciliary papilla; *CT*, connective tissue; *I*, iris; *L*, lens; *ON*, optic nerve; *R*, retina; *S*, scleral cartilage; *SL*, suspensory ligament; *SO*, scleral ossicles; *V*, vortex vein; *Z*, zonule.

The retina is primitive in its structure (Dogiel, 1883; Schiefferdecker, 1886). The pigmentary epithelium, resembling that of *Selachian*, is practically devoid of pigment throughout the sensory retina in order that the mirror effect of the tapetum may be effective

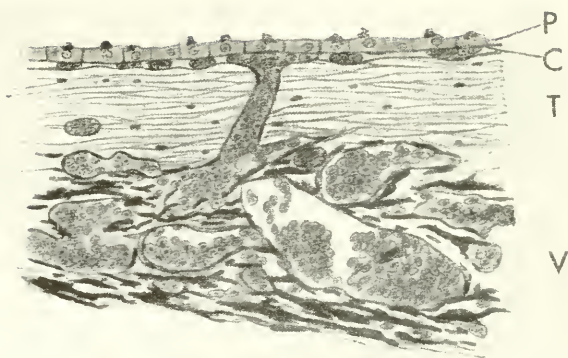
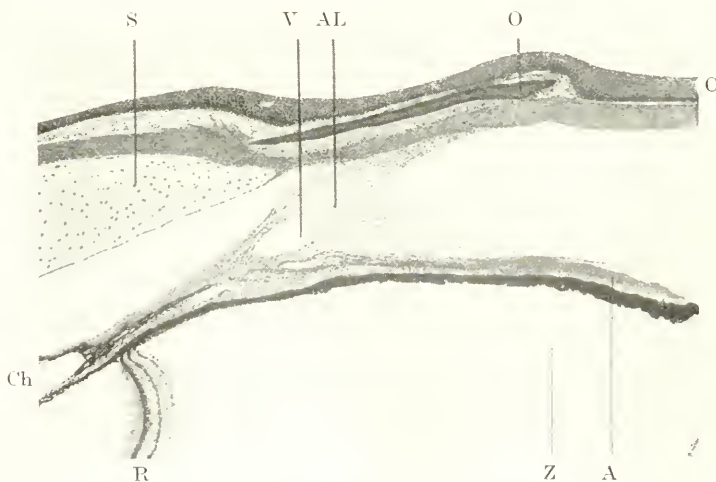


FIG. 371.—THE TAPETUM OF CHONDROSTEANS.

The choroid of the sturgeon, *Acipenser*. The tapetum, *T*, lying between the choriocapillaris, *C*, and the vessel layer of the choroid, *V*, pierced by a large vessel from the latter to supply the former. The pigment epithelium, *P*, is devoid of pigment apart from small accumulations on its inner surface (a drawing after Mürr).

(Fig. 371) ; in the ciliary region it becomes heavily pigmented. The sensory retina is characterized by the large size of the horizontal cells, the virtual absence of a distinct inner nuclear layer, and the small number of ganglion cells which remain isolated without forming a

FIG. 372.—THE ANGLE OF THE ANTERIOR CHAMBER OF *ACIPENSER*.

A, argentea of iris ; *AL*, annular ligament ; *C*, cornea ; *Ch*, choroid ; *O*, osseous plaques ; *R*, retina ; *S*, scleral cartilage ; *V*, vessel behind annular ligament ; *Z*, zonule (from a drawing by Rochon-Duvigneaud, *Les Yeux et la Vision des Vertébrés* ; Masson et Cie).

definite layer. Both rods and cones are present ; the rods, long and thick, the cones single and containing colourless oil-droplets—the most primitive Vertebrate species in which these appear. There is no area centralis (Fig. 373).

In general it would appear that the eye of the sturgeon represents a transitional phase between the selachian and teleostean eye with more affinities for the former than the latter. The scleral cartilage is of the selachian type, but the subconjunctival bony plaques are an innovation. The argentea, present in Selachians as a rudimentary layer in the iris, is continued throughout the uveal tract. The foetal fissure persists but the retractor lentis muscle of Teleosts has not yet evolved. The immobility of the iris is more primitive even than in Selachians. The general architecture of the retina is selachian in its simplicity rather than teleostean in its perfection ; but the appearance of oil-droplets at an early stage among Vertebrates in the cones is an interesting phylogenetic innovation.

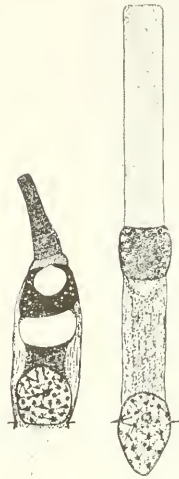


FIG. 373. — THE VISUAL ELEMENTS OF *ACIPENSER FULVERCENS*.

A cone (containing a colourless oil-droplet) and a long thick rod ($\times 1,000$) (Gordon Walls).

The POLYPTERINI are represented only by two archaic types both inhabiting African waters—*Polypterus* and *Calamoichthys*. The eyes of the former were studied by Leydig (1854) and Rochon-Duvigneaud (1943), and the latter also by Rochon-Duvigneaud (1943). In *Polypterus* the eye appears to resemble that of *Amia*¹ and is of the teleostean type. The cornea is not divided and Bowman's membrane is lacking ; there is a continuous scleral cartilage without bony enforcement, an argentea lining the choroid but poorly represented in the iris, and a spherical lens. There is no open foetal fissure, no choroidal gland but an extensive membrana vasculosa retinae, no pupillary musculature, no tensor choroideae, and a poorly developed annular ligament. The rods are large, the cones are single and contain oil-droplets, the ganglion cells are scanty and do not form a definite layer, and the optic nerve which has the lamellar structure of the teleostean type, is branched with multiple optic discs (Studnicka, 1898).



Polypterus



Calamoichthys

The eye of *Calamoichthys* is of the same general structure but, according to Rochon-Duvigneaud (1943), the retina is exceedingly thin, with few cellular elements of any kind, the short and thick visual cells being of one type only having the morphological characteristics of cones some of which are provided with an oil-droplet.

¹ p. 321.

THE HOLOSTEAN EYE

TWO EXTANT REPRESENTATIVES are all that remain of the very ancient group of Holosteans, both confined to North American waters—the bow-fin, *Amia*, and the gar-pike, *Lepidosteus*. As the progenitors of Teleosteans, it is to be expected that their eyes resemble the teleostean type (Ziegenhagen, 1895 ; Franz, 1934).

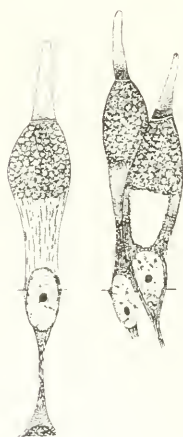
FIGS. 374 AND 375.—THE VISUAL ELEMENTS OF *AMIA CALVA*.*Amia**Lepidosteus*

FIG. 374.



FIG. 375.

FIG. 374.—The cones of *Amia* ; a single cone and a double cone.

FIG. 375.—A rod of *Amia* ($\times 1,000$) (Gordon Walls).

The sclera has a complete cup of hyaline cartilage ; the cornea is tinted a yellow colour (Walls and Judd, 1933) and the laminated substantia propria is homogeneous ; the annular ligament at the angle of the anterior chamber is marked. The choroid has typical teleostean features with an argentea, a large choroidal gland (in *Amia* only), a falciform process and a campanula with an ectodermal muscle ; there is a dorsal suspensory ligament and (as in some Teleosts) a membrana vasculosa retinae, the vessels of which, however, enter at the mid-ventral point of the ora. The iris, over which the argentea is prolonged,

is devoid of muscles and the pupil is slightly oval with the long axis vertical, moving only passively when the lens moves in accommodation. The retina is typically teleostean, and contains double cones (Fig. 374) ; there are, however, no twin cones nor an area centralis. The optic nerve is of the teleostean type, with a broad ribbon of nerve fibres folded over itself in pleats within the tubular sheath.

ANOMALIES IN THE EYES OF FISHES

In a group so heterogeneous as the Fishes it is not surprising that many modifications to the general form arise ; some of the most important of these deserve a passing note.

THE TUBULAR OR TELESCOPIC EYE

We have already seen that lack of illumination in the abyssal depths has led to the development of an immensely large lens to

FIGS. 376 TO 379.—THE TUBULAR EYES OF DEEP-SEA FISH.

FIGS. 376 AND 377.—The Hatchet Fish, *Argyropspectus*.

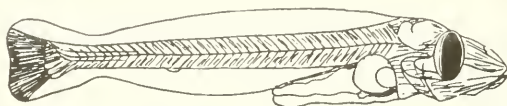


FIG. 376.—In the larva the eye is directed forwards.

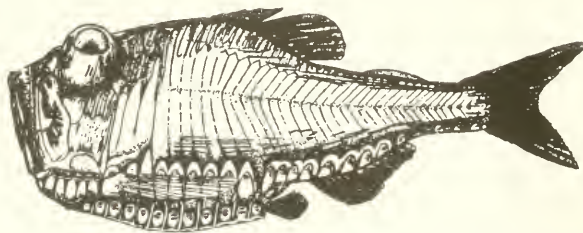


FIG. 377.—In the adult the eyes are tubular and upward-looking ; the body is covered with luminous organs giving the scales a silvery gleam (compare Fig. 892) (after Goode and Bean).

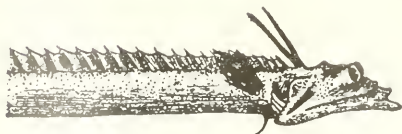


FIG. 378.—*Stylophorus paradoxus*. An inhabitant of the deep Atlantic. The eyes are directed forwards and slightly upwards (after Goode and Bean, 1896).



FIG. 379.—The giant-tailed fish, *Giganturus chuni*. An inhabitant of the deep Atlantic. The eyes are directed straight forwards (from the Valdivia Reports).

collect as much as possible of the small amount of light available, and, indeed, in some species in order to accommodate this structure the eye may attain a size more than half the length of the head (*Bathylagus*, *Zenion*, etc.)—relatively the largest eyes of all Vertebrates. A much more economic arrangement may therefore be adopted by some deep-sea Teleosts in the TUBULAR EYE (or telescopic eye) wherein the unnecessary volume of a relatively circular organ has been eliminated in favour of a cylindrical shape, the axial portions only of the globe

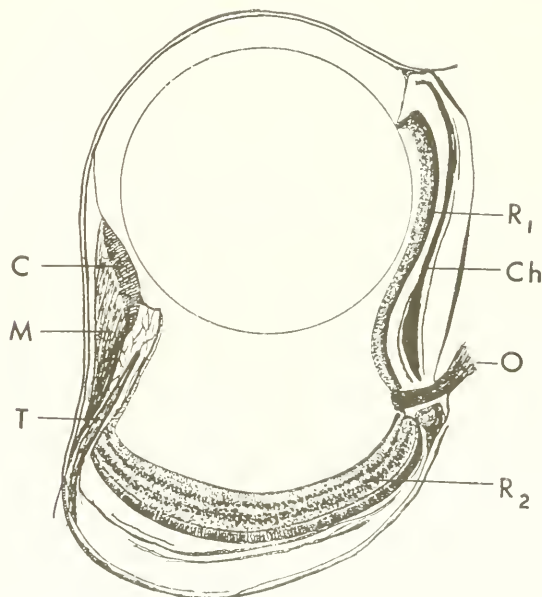
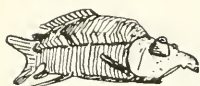


FIG. 380.—THE TUBULAR EYE OF A DEEP-SEA FISH.

The eye of *Scopelarchus analis*, an inhabitant of the deep Atlantic and Indian oceans, in longitudinal section, showing the enormous lens and the general distortion of the globe. *C*, the lens cushion moved by a muscle, *M*, which accommodates for distance; *T*, tapetum; *Ch*, choroid; *R*₁, accessory retina; *R*₂, principal retina; *O*, optic nerve (after Chun).

being retained in order that the enormous lens might be accommodated in an organ which had not become impossibly large (Fig. 380). In such an eye the lens occupies the entire anterior portion of the globe and the iris is eliminated. In order to increase the visual field, however, the "principal retina" lying at the bottom of the tube may be reinforced by an "accessory retina" continued up one side opposite which the sclera remains transparent (Brauer, 1908). In these species the eye is initially normal in form and becomes tubular as growth proceeds (the hatchet fish, *Argyropelecus*, etc., Contino, 1939) (Figs. 376–7); in some the eyes are eventually directed forwards (*Giganturus*) (Fig. 379) or

*Opisthoproctus*

forwards and upwards (*Stylophorus*) (Fig. 378); in others, upwards (*Argyropelecus*, *Opisthoproctus*), in which case the sclera on the dorsal aspect becomes transparent and the ventral part of the retina assumes the function of the "principal retina", so that the optic nerve emerges from its edge instead of from its centre (Fig. 380).

The intimate structure of such an eye is seen in Fig. 380. The principal retina is well formed, the accessory retina atrophied, while the optic nerve

emerges laterally between the two. To move the immense lens there is a lens pad controlled to some extent by muscles which enable the eye to be focused on a distant object. On the whole, however, such eyes are myopic and specifically adapted for the perception of the small amount of light available, although it is possible that a sufficiently adequate image of prey may be appreciated to allow its capture when it approaches so closely that it can be snapped at.



FIG. 381.—THE "TELESCOPE-EYED" GOLDFISH (Zool. Soc., London).

Such an eye is found in several species in addition to *Giganturus*, *Stylophorus* and *Argyropelecus*—some relatives of the deep-sea salmonids, *Dolichopteryx* and *Winteria*, and some of the deep-sea lantern fishes (Myctophidæ), such as some species of *Evermannella* and *Scopelarchus*.

It is interesting that a "deformed" tubular eye of this type can be produced by artificial selection in breeding, as is seen, for example, in the "telescope-eyed" goldfish (Fig. 381).

THE AMPHIBIOUS EYE

Fishes which require to see both under water and in air are presented with the difficulty of combining two very different optical requirements. In many cases there seems to be little structural adaptation to the comparative myopia of aerial and the hypermetropia of aquatic vision unless the accommodative range is unusually great. Very interesting modifications, however, occur in at least one species—*Anableps tetraphthalmus*, the "Cuatro ojos" which swims sedately in quiet waters of South and Central America in such a way that the water-line cuts across the middle of the prominently raised eyes (Figs. 382 to 384). This extraordinarily interesting eye has received a considerable amount of study from the time of Artedi (1758) and Soemmerring (1818) (Schneider and v. Orelli, 1908; Arruga, 1941). It is provided with two distinct optical systems, the upper for aerial, the lower for aquatic vision. The cornea is divided into two segments by a densely pigmented horizontal raphe, and the iris is similarly divided so that two pupillary apertures are present; the lens is fusiform in shape, its short axis refracting rays onto the lower part of the retina

from the upper (aerial) pupil and its long axis refracting rays from the lower (aquatic) pupil onto the upper part (Fig. 385). It would seem therefore that both aerial and aquatic objects are focused simultaneously on different parts of the retina, the dioptrics in either case

FIGS. 382 TO 384.—*ANABLEPS TETROPHthalmus*.

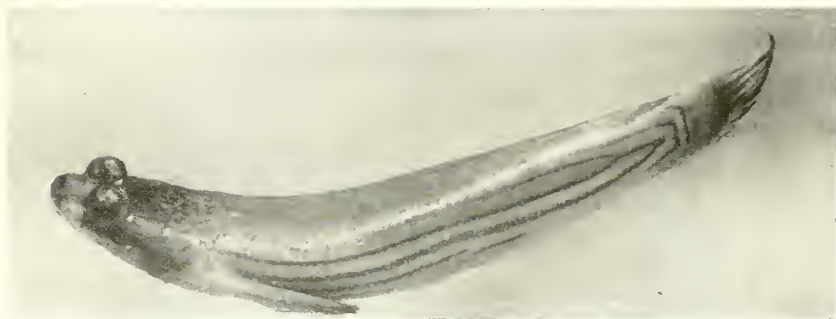


FIG. 382.



FIG. 383.



FIG. 384.

Showing the horizontal division of the pupil, the upper part being adapted for vision in the air, the lower part in the water. A Brazilian specimen (N. Ambache).

being catered for by the peculiar shape of the lens (Fig. 766). The four-eyed blenny, *Dialommus fuscus*, which frequents rocks between the tide-marks, has a similar division of its otherwise heavily pigmented cornea into two clear areas, but the pupillary aperture is single (Breder and Gresser, 1939). A pupil which is practically double, however, is seen in the large serpent eel of New Zealand, *Leptognathus*, an inhabitant of the deep seas which burrows in the mud (Prince, 1949) (Fig. 340).

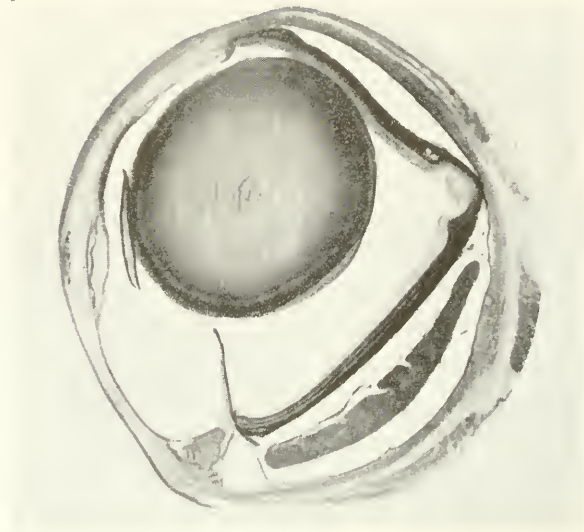


FIG. 385.—THE EYE OF *AYABLEPS* IN VERTICAL SECTION.

The immense cornea (to the left) occupies $\frac{2}{5}$ ths of the surface of the globe and is bisected horizontally across the middle. Internal to the bisection is seen the part of the iris which spans the anterior chamber transversely to create the two pupils, the upper for aerial, the lower for aquatic vision. In the lower part of the choroid is seen the huge choroidal gland lying between the detached retina and the sclera (H. Arruga).

STALKED EYES

In a few Teleosteans the eyes are set prominently on stalks. An example of this is the mud-skipper, *Periophthalmus*, found in the tropical swamps of Asia, Africa and Polynesia, which skips upon the mud on its stiff pectoral fins seeking insects (Fig. 386). The eyes are retractile and can be withdrawn for protection when they are covered by puckered skin-folds; they are raised by a hammock formed by a crossing of the inferior rectus and inferior oblique muscles. When

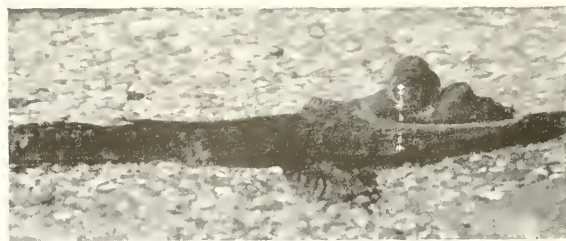


FIG. 386.—THE MUD-SKIPPER, *PERIOPHTHALMUS*.

The water-line cuts the head of the fish just beneath the eyes; the corneal reflex is seen reflected immediately underneath on the surface of the water (photograph by Michael Soley).

accommodating maximally the eyes are focused for aerial vision, and to adapt the vision to the bright sunlight on land. the inferior part of the retina is populated only by cones, while rods become increasingly more numerous in its upper half.

The hammerhead shark, *Sphyrna zygaena*, has eyes which are located far laterally at the ends of the "hammers", and show a peculiar adaptation of the extra-ocular muscles (Fig. 388). The elongation of the orbits in the lateral direction would ordinarily necessitate muscles

FIGS. 387 AND 388.—THE HAMMERHEAD SHARK, *SPHYRNA ZYGAENA*.

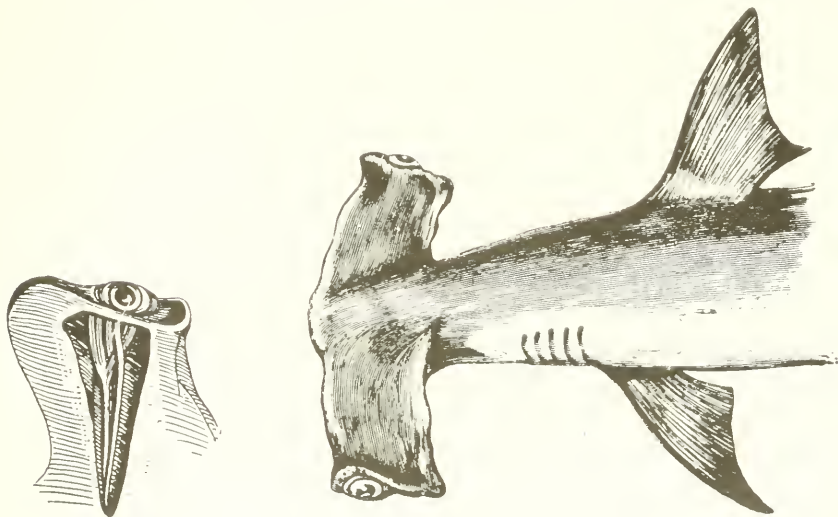


FIG. 387.

FIG. 387.—The dissected orbit.

FIG. 388.

FIG. 388.—The head, showing the extraordinarily elongated orbits giving the impression of the heads of two symmetrical hammers on which the eyes are perched (Bland-Sutton's *Lectures and Essays*; Heinemann).

of quite unusual length; these, however, are no longer proportionately than in any other species of shark and, instead of being inserted at the apex of the orbit, take origin from a common tendon running parallel with the optic nerve throughout the inner three-quarters of the orbit (Bland-Sutton, 1920) (Fig. 387). The bonnet-shark, *Sphyrna tiburo*, has a head of a somewhat similar configuration, taking the shape of a crescent with the eyes situated on the widest part.

The most extraordinary stalked eye among Teleosts, however, is seen in the *Stylophthalmus paradoxus*, the larva of the deep-sea *Idiacanthus* (Brauer, 1908; Beebe, 1934). The eye is perched on an enormously long, freely movable stalk which contains the optic nerve and filamentous muscles and is supported by a cartilaginous rod



Sphyrna tiburo

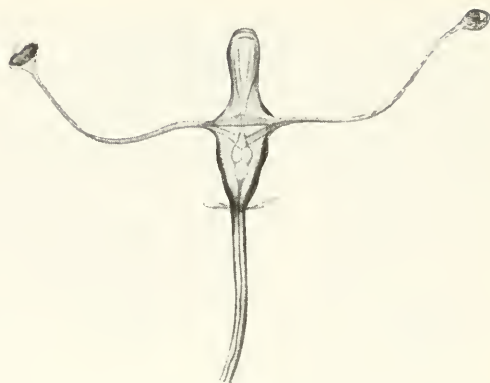


FIG. 389.—THE STALKED-EYED TELEOST, *STYLOPHTHALMUS PARADOXUS*, THE LARVA OF *IDIACANTHUS*.

Showing the eyes at the termination of the two stalks (after Brauer).

FIGS. 390 TO 392.—DIAGRAM OF THE DEVELOPMENT OF THE TELEOST, *IDIACANTHUS FASCIOLA* (after Beebe).

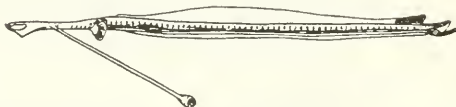


FIG. 390.—Young stalk-eyed larva, *Stylophthalmus paradoxus*, 16 mm. long.

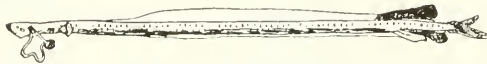


FIG. 391.—Larva with degenerating eye, 40 mm. long.

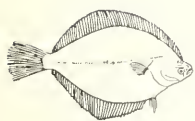


FIG. 392.—Adult male *Idiacanthus*.

rooted on the skull (Figs. 389, 390). In the adult the eyes retract into a normal position, the cartilaginous rod becoming folded upon itself into a tangled mass in the orbit (Figs. 391-2).

THE MIGRATORY EYE

This is a curious phenomenon seen in the many types of flat-fishes. In the Selachians which are compressed dorso-ventrally, the two eyes migrate equally towards the dorsal mid-line so that they are directed more or less skywards. The flat Teleosteans (which include such food-fishes as halibut, plaice, turbot and sole) when young have the normal torpedo-shaped body of a fish and they swim with the usual orientation with laterally directed eyes; but at a later stage when



Plaice



Sole

they remain constantly at the bottom of the sea, they lie upon one side so that the eye which finds itself underneath (the left eye in the sole, the right in the turbot) migrates to the upper side and eventually lies alongside the other in a hole formed in the frontal bone. The two orbits, like the rest of the head, are consequently very asymmetrical. In one species (*Psettodes*) the migration is incomplete so that the migratory eye does not reach the top of the head. In this way the flat-fish attains a wide binocular field above¹, and in many species the eyes are raised on ocular turrets so that vision is still possible when most of the body of the fish is concealed under sand. In order to avoid dazzle in the upward-looking eyes of these flat-fishes, as well as in some other bottom fishes, an expansile pupillary opereulum is developed comparable to that found in Batoidei.² This structure may be small, as in the star-gazer, *Uranoscopus* (Fig. 393) or so large that it practically occludes the entire pupil, as in the cat-fish, *Plecostomus* (Fig. 394).

*Psettodes*

FIG. 393.



FIG. 394.

FIG. 393.—THE PUPIL OF THE STARGAZER, *URANOSCOPIUS*.

FIG. 394.—THE PUPIL OF THE CATFISH, *PLECOSTOMUS*.

- Abelsdorff. *Arch. Anat. Physiol., Abt. Physiol.*, 345 (1896).
- Addario. *Monit. Zool. ital.*, **13**, 16 (1903).
- Allen. *Anat. Rec.*, **103**, 205 (1949).
- Allis. *J. Anat.*, **56**, 189 (1922).
- Angelucci. *Arch. mikr. Anat.*, **19**, 152 (1881).
- Arey. Cowdry's *Special Cytology*, N.Y., **2**, 889 (1928).
- Arruga. *O Olho do Quatrilhos*, Barcelona (1941).
- Artedi. *Seba's Rerum naturalium thesauri descriptione*, Amstel., **3** (1758).
- Baecker. *Z. mikr. Anat. Forsch.*, **26**, 412 (1931).
- Ballowitz. *Anat. Anz.*, **45**, 91 (1913).
- Barnett. *J. Anat.*, **85**, 113 (1951).
- Barraquer-Cerero. *Arch. Soc. Oftal. hisp.-amer.*, **12**, 507 (1952).
- Beebe. *Zoologica* (N.Y.), **16**, 149 (1934).
- Beer. *Pflügers Arch. ges. Physiol.*, **58**, 523 (1894).
- Bland-Sutton. *Selected Lectures and Essays*, 4th Ed., London, 76 (1920).
- Bourguignon and Verrier. *Bull. Soc. ophthalm. Paris*, 273 (1930).
- Brauer. *Wiss. Ergeb. dtsch. Tiefsee Exped. "Valdivia"*, **15**, 266 (1908).
- Breder and Gresser. *Zoologica* (N.Y.), **24**, 239 (1939).
- Brown-Séquard. *C. R. Acad. Sci. (Paris)*, **25**, 482, 508 (1847).
- J. Physiol. Path. gén.*, **2**, 281 (1859).
- Brücke. *Arch. Anat. Physiol.*, 387 (1845).
- Bruesch and Arey. *J. comp. Neurol.*, **77**, 631 (1942).
- Cajal. *La Cellule*, **9**, 119 (1893).
- Trav. Lab. biol. Madrid*, **28**, Appendix, 1 (1933).
- Carrère. *Les muscles de l'iris chez les Sélaciens*, Montpellier (1923).
- Carrière, J. *Die Sehorgane d. Thiere, Vergl.-anat. dargestellt*, München (1885).
- Chrustschoff. *Z. mikr. Anat. Forsch.*, **7**, 121 (1926).
- Contino. *v. Graefes Arch. Ophthalm.*, **140**, 390 (1939).
- Corning. *Morphol. Jb.*, **29**, 94 (1900).
- Cuvier. *Leçons d'anat. comparée*, Paris (1805).
- Denissenko. *Arch. mikr. Anat.*, **19**, 395 (1881); **21**, 1 (1882).
- Detwiler. *Vertebrate Photoreceptors*, N.Y. (1943).
- Deyl. *Anat. Anz.*, **11**, 8 (1895).
- Dobrowolsky. *Arch. Anat. Physiol.*, 208 (1871).
- Dogiel. *Arch. mikr. Anat.*, **22**, 419 (1883).
- Edinger. *Anat. Anz.*, **66**, 172 (1928).
- Erdl. *Disquisitiones de glandula choroidali*, Monarchi (1839).
- Faravelli. *Atti roy. Acad. Sci.*, Torino, **26**, 268 (1890-91).
- Franz. *Jena. Z. Naturwiss.*, **40**, 697 (1905); **41**, 429 (1906).
- Arch. vergl. Ophthalm.*, **1**, 427 (1910).

¹ p. 679.² p. 287.

- Franz. *Zool. Jb., Abt. Zool. Physiol.*, **49**, 323 (1931).
- Bolk's *Hb. d. vergl. Anat. d. Wirbeltiere*, Berlin, **2** (ii), 1009 (1934).
- Garten. *Graefe-Saemisch Hb. d. ges. Augenheilk.*, II, **3**, Kap. 12, Anhang (1907).
- Winterstein's *Hb. d. vergl. Physiol.*, **3**, 105 (1910).
- Giacomelli. *Atti Cong. Soc. Oftal. ital.*, 533 (1935).
- Greeff. *Graefe-Saemisch Hb. d. ges. Augenheilk.*, II, **1**, (2), Kap. 5, 74 (1899).
- Grynfeldt. *Arch. Anat. micr.*, Paris, **12**, 475 (1910).
- C. R. Acad. Sci. (Paris), **150**, 420 (1910).
- Bull. Mens. Acad. Sci. Lettr. de Montpellier, 210 (1911).
- Grynfeldt and Demelle. *Bibl. Anat.*, **18**, 17 (1908).
- Haller. *Acad. d. Sci.*, 76 (1762).
- Opera anatomici minora*, Lusanne (1768).
- Hannover. *Arch. Anat. Physiol. wiss. Med.*, 320 (1840).
- Das Auge*, Leipzig (1852).
- La rétine de l'homme et des vertébrés*, Copenhagen (1876).
- Harman. *J. Anat. Physiol.*, **34**, 1 (1899).
- Trans. ophthal. Soc. U.K.*, **23**, 356 (1903).
- Harms. *Z. wiss. Zool.*, **131**, 157 (1928).
- Hein. *T. Ned. Dierk. Vereen.*, **12**, 238 (1913).
- v. Hess. Winterstein's *Hb. d. vergl. Physiol.*, Jena, **4**, 1 (1912).
- Hesse. *Zool. Jb., Abt. Syst.*, Suppl. **7**, 471 (1904).
- Hogben and Landgrebe. *Proc. roy. Soc. B*, **128**, 317 (1940).
- Hosch. *Arch. mikr. Anat.*, **64**, 99 (1904).
- Kahmann. *Zool. Anz.*, **106**, 49 (1934).
- v. Graefes *Arch. Ophthal.*, **135**, 265 (1936).
- Karsten. *Jena. Z. Naturwiss.*, **59**, 115 (1923).
- Kerr. *Quart. J. Med. Sci.*, **46**, 417 (1902).
- Textbook of Embryology*, London, **2** (1919).
- Koch. *Atti Soc. Oftal. ital.*, **12**, 108 (1950).
- Ann. Ottal.*, **78**, 881 (1952).
- Atti Soc. Oftal. Lombarda*, **7**, 197 (1952).
- Ophthalmologica*, **126**, 58 (1953).
- Kolmer. *Anat. Anz.*, **44**, 183 (1913).
- Krause, W. Henle's *Hb. syst. Anat. d. Menschen*, **3** (1876).
- Internat. Mschr. Anat. Histol.*, **3**, 8, 41 (1886); **6**, 206, 250 (1889).
- Lauber. *Anat. Hefte*, **18**, 369 (1901).
- Leuckart. *Graefe-Saemisch Hb. d. ges. Augenheilk.*, I, **2** (2), 145 (1876).
- Leydig. *Anat. Hist. Untersuch. ü. Fische u. Amphibien*, Berlin (1853).
- Z. wiss. Zool.*, **5**, 40 (1854).
- Loewen. *Arch. Anat. (Paris)*, **25**, 167 (1935).
- Lumbroso. *Ric. Morfol.*, **14**, 163, 257 (1935).
- Lyall. *Nature* (Lond.), **177**, 1086 (1956).
- Quart. J. micros. Sci.*, **98**, 189 (1957).
- McEwan. *Acta Zool.*, **19**, 427 (1938).
- Magnus. *Z. Biol.*, **20**, 567 (1899).
- Mann. *Trans. ophthal. Soc. U.K.*, **49**, 353 (1929).
- Proc. zool. Soc. Lond.*, **21**, 355 (1931).
- Matthiessen. *Pflügers Arch. ges. Physiol.*, **38**, 521 (1886).
- Mayhoff. *Zool. Anz.*, **39**, 78 (1912).
- Mayou. *Brit. J. Ophthal.*, **17**, 477 (1933).
- Meador. *J. Morph.*, **59**, 163 (1936).
- Michaelson. *Retinal Circulation in Man and Animals*, Ill. (1954).
- Millot. *Le pigment purique chez les vertébrés inférieurs*, Paris (1923).
- Millot and Carasso. *C.R. Acad. Sci. (Paris)*, **241**, 576 (1955).
- Moore. *J. comp. Neurol.*, **80**, 369 (1944).
- Moore, Pollock and Lima. *J. comp. Neurol.*, **53**, 289 (1950).
- Müller, Heinrich. *Z. wiss. Zool.*, **8**, 1 (1857); **9**, 147 (1858).
- Gesammelte u. hinterlassene Schriften z. Anat. u. Physiol. d. Auges*, Leipzig (1872).
- Müller, H. *Z. vergl. Physiol.*, **37**, 1 (1954).
- Müller, J. *Arch. Anat. Physiol.*, 101 (1840).
- Müller, W. *Beit. Anat. Physiol. (Festgabe C. Ludwig)*, Leipzig, **2** (1875).
- Mürr. *Z. Zellforsch. mikr. Anat.*, **6**, 315 (1927).
- Neunmayer. *Arch. mikr. Anat.*, **48**, 83 (1897).
- Nussbaum. *Arch. mikr. Anat.*, **58**, 199 (1901).
- Parker. *Bull. Mus. comp. Zool.*, **40**, 221 (1904).
- Prince. *Visual Development*, Edin. (1949).
- J. comp. Neurol.*, **103**, 541 (1955).
- Rabl. *Z. wiss. Zool.*, **63**, 496 (1898).
- Ueber d. Bau u. d. Entwicklung d. Linse*, Leipzig (1900).
- Rasquin. *Physiol. Zool.*, **22**, 131 (1949).
- Remotti. *Ric. Morfol.*, **9**, 89 (1929).
- Retzius. *Biologische Untersuchungen*, Stockholm, **1**, 89 (1881); **12**, 55 (1905).
- Ridewood. *J. Anat. Physiol.*, **33**, 228 (1898).
- Rochon-Duvigneaud. *Ann. Oculist. (Paris)*, **153**, 185 (1916).
- Les yeux et la vision des vertébrés*, Paris (1943).
- Schaffer. *Z. mikr. Anat. Forsch.*, **18**, 37 (1929).
- Schaper. *Festschr. z. 70 Geburt. von Kupffer*, 1 (1899).
- Schiefferdecker. *Arch. mikr. Anat.*, **28**, 305 (1886).
- Anat. Anz.*, **2**, 381 (1887).
- Schnaudigel. *Ber. dtsh. ophthal. Ges. Heidel.*, **32**, 329 (1905).

- Schneider and v. Orelli. *Mitt. d. naturf. Ges. Berne*, 87 (1908).
- Schultze, M. *Arch. mikr. Anat.*, **2**, 175 (1866); **3**, 215 (1867).
- Schultze, O. *Zur Entwicklungsges. d. Gefässsystems in Säugetiere*, Wurzburg (1892).
- Shearer. *J. comp. Neurol.*, **8**, 209 (1898).
- Smelser and Chen. *Acta XIII Internat. Cong. Ophthal.*, Montreal-N.Y., **1**, 490 (1954).
- Soemmerring, D. W. *De oculorum hominis animaliumque etc.*, Goettingen, p. 68 (1818).
- Strampelli. *Ric. Morfol.*, **13**, 47 (1934).
- Studnicka. *Jena. Z. Naturwiss.*, **31**, 1 (1898).
- Sverdllick. *Acta XIII Internat. Cong. Ophthal.*, Montreal-N.Y., **3**, 1959 (1954).
- v. Szily. *v. Graefes Arch. Ophthal.*, **109**, 1 (1922).
- Teulières and Beauvieux. *Arch. Ophtal.* (Paris), **48**, 465 (1931).
- Tretjakoff. *Morphol. Jb.*, **56**, 402 (1926). *Z. wiss. Zool.*, **127**, 645 (1926); **137**, 550 (1930).
- Ucke. *Diss.*, Dorpat (1891).
- Verrier. *Bull. Mus. Paris*, **33**, 361 (1927). *Bull. Biol. France Belg.*, Suppl. **11**, 137 (1928).
- Ann. Sci. nat. Zool.*, **13**, 5 (1930); **18**, 205 (1935).
- Bull. Soc. zool. France*, **58**, 62 (1933).
- C. R. Soc. Biol.* (Paris), **113**, 134 (1933). *Les yeux et la vision*, Paris (1938).
- Vilter. *C. R. Soc. Biol.* (Paris), **141**, 344, 346 (1947); **142**, 292 (1948); **144**, 200 (1950); **145**, 52, 54 (1951); **147**, 1937 (1953); **148**, 59, 327, 466 (1954).
- Virchow. *Morphol. Jb.*, **7**, 573 (1882). *Arch. Anat. Physiol., Physiol. Abt.*, 169 (1890).
- de Waele. *Bull. Mus. Hist. nat.*, 378 (1900).
- Walls. *The Vertebrate Eye*, Michigan (1942).
- Walls and Judd. *Brit. J. Ophthal.*, **17**, 641 (1933).
- Woelfflin. *Klin. Mbl. Augenheilk.*, **126**, 348 (1955).
- Wunder. *Z. vergl. Physiol.*, **3**, 1, 595 (1925); **4**, 22 (1926); **11**, 749 (1930). *Z. wiss. Biol., Abt. C3*, 1 (1926).
- Yamasaki. *Yokohama Med. Bull.*, **4**, 325 (1953); **5**, 304 (1954).
- Yatabe. *Keijo J. Med.*, **3**, 15 (1932).
- Young. *Proc. roy. Soc. B*, **112**, 228 (1933).
- Ziegenhagen. *Beit. z. Anat. d. Fischeaugen*, Berlin (1895).