CHAPTER X

THE EYES OF CYCLOSTOMES

Although he made a classical description of the eyes of all classes of Vertebrates except Cyclostomes, I am introducing this chapter which is the first of a series dealing with the structure of the eyes of Vertebrates with the portrait of DETMAR WILHELM SOEMMERRING (1793–1871) (Fig. 269) in view of the fact that he was one of the earliest writers to make a systematic study of this subject. It is true that many incidental observations had been made on the finer structure of the eyes of different Vertebrates by such investigators as van Leeuwenhoek,[1] Zinn [2] and Young,[3] while compendia had been published by such authors as Blumenbach,[4] Albers,[5] and Cuvier [6]; but none is so delightful to read as is the thesis written in Latin which brought Soemmerring his doctorate in Göttingen in 1816, and was published in 1818 under the title *De oculorum hominis animaliumque sectione horizontali commentatio*; the illustrations are so beautiful that several of them have been reproduced in the following chapters. D. W. Soemmerring, the son of an equally distinguished German ophthalmologist, S. T. von Soemmerring (who, it will be remembered, first described the macula lutea as a hole in the retina), was born in Frankfurt where in later life he practised for many years and where his jubilee as a doctor was officially celebrated in 1866. He is also remembered ophthalmologically for two particular observations —a description of the organic changes in the eye after the operation for cataract in which he described the annular remnant of the lens now universally known as Soemmerring's ring (1828), and the first description of a living cysticercus in the human eye (1830).

The CYCLOSTOMES (κύκλος, round; στόμα, a mouth), so called because of their round, jawless, suctorial mouths which differentiate them from all other Vertebrates, are the only surviving representatives of the large class of AGNATHA (ἀ, privative; γνάθος, jaw) which flourished in great variety and numbers during Palæozoic times and are now with this exception extinct. They are freely-swimming worm-like "pre-fishes" of extreme antiquity, essentially primitive in their structure and differing in many ways from true Fishes, principally in the absence of jaws, by the single olfactory organ and by the absence of paired fins. Today they are represented by two existing types and a few others like them—the *hagfishes* (slime-eels) and the *lampreys*. The eyes of the former, buried deeply within the skin, are degenerate and sightless and are described at a later stage[7]; those of the latter, at first buried and later coming to the surface, constitute the most

[1] *Epistolæ physiologicæ*, Delphis, 1719.
[2] *Comment. Soc. Sci.*, Göttingen, 1754.
[3] *Philos. Trans.*, 1793.
[4] *Vergl. Anat.*, 1784.
[5] *Beyt. z. Anat. u. Physiol. d. Thiere*, 1802.
[6] *Leçons d'anat. comparée*, Paris, 1805.
[7] p. 734.

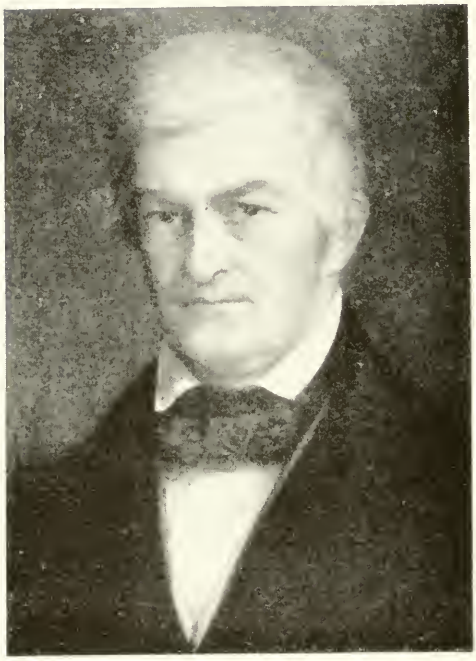

Fig. 269.—D. W. Soemmerring (1793–1871).

primitive type of vertebrate eye showing characteristics differing markedly from those of Fishes.

THE LAMPREYS (PETROMYZONIDÆ)

The lampreys are large eel-like creatures found mainly in the seas and rivers of the northern hemisphere ; the sea lamprey (*Petromyzon marinus*), about 3 feet in length, and the fresh-water river lampern (*Lampetra fluviatilis*), about 2 feet in length, eat worms and small crustaceans and are also ectoparasites on living fishes to which they attach themselves and feed by rasping off the flesh. From the latter species smaller brook lamperns (sand-prides) have presumably been derived ; these do all their feeding as larvæ and after metamorphosis to the adult form, breed and then die. Related genera are *Mordacia* and *Geotria* from the coasts of Chile and Australasia, and *Ichthyomyzon* from the western coasts of North America (Fig. 270).

The life-cycle of the lamprey is interesting and complex. The larva, or *Ammocœtes* (sometimes known as the " pride " when it was

FIG. 270.—THE SEA LAMPREY, *PETROMYZON MARINUS*.

There are two unpaired median fins and a relatively large eye ; behind the eye are seven point-like gill-slits. For the head of the lamprey, see Fig. 862.

thought to be a different species), is a small creature without a sucking mouth and with a solid spinal cord in which a medullary cavity subsequently develops [1] ; the eyes are extremely rudimentary and lie beneath the skin. Before metamorphosis the larva burrows in mud and the non-functional eyes are covered with opaque integument. At metamorphosis during the latter half of July, at the age of 2 to 4 years, great changes occur as the ammocœtes leaves the mud or sand and transforms into the eel-like adult, changes which include the development and emergence of the eyes. The simple and relatively undifferentiated retina of the larva (retina A) rapidly becomes transformed into the functional adult tissue (retina B) and as it does so the overlying skin atrophies and becomes transparent. The adult organ is rapidly formed, neither regressive, atrophied nor degenerate in type, but primitive in nature and embryonic in certain characteristics, particularly in the structure of the optic nerve.

It is interesting that the animal also possesses pineal and parietal " eyes," a subject which will be fully discussed in a later chapter.[2]

[1] Compare p. 239, footnote. [2] p. 711.

THE AMMOCŒTE EYE

Since the original description by W. Müller (1875), several studies have been made of the ammocœte eye. The youngest specimen described was that of Ida Mann (1928) who figured a simple optic vesicle evaginated from the anterior cerebral vesicle lying close underneath the surface ectoderm (Fig. 271). At this early stage there was neither vitreous nor lens, the outer layer of the vesicle

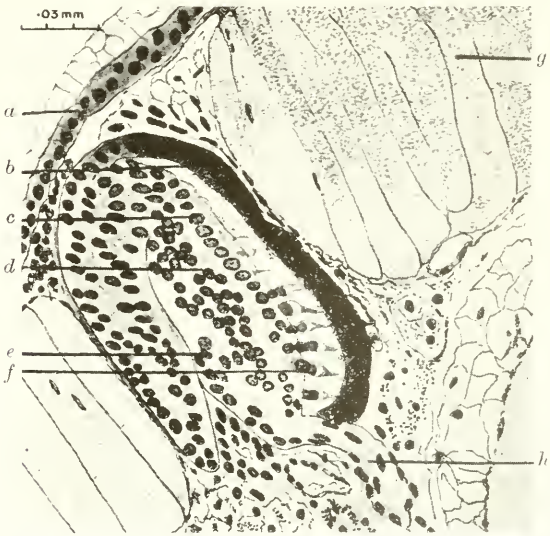

FIG. 271.—SECTION THROUGH THE EYE OF THE AMMOCŒTES (THE LARVA OF *PETROMYZON FLUVIATILIS*).

There is neither vitreous nor lens ; the optic cup is closely folded upon itself, the outer layer being pigmented and the inner showing a considerable degree of differentiation.

a, surface epithelium of the head ; *b*, pigmented outer layer of the optic cup ; *c*, nuclei of the visual cells ; *d*, nuclei of bipolar cells ; *e*, ganglion cells with nerve fibres arising from them ; *f*, visual cells ; *g*, muscle mass of head ; *h*, optic nerve (Ida Mann).

being pigmented and the inner showing differentiation into the three layers of cells characteristic of the vertebrate visual retina—visual cells (indistinguishable either as rods or cones), bipolar cells and ganglion cells the axons of which constitute the optic nerve. In somewhat older larvæ (5–10 mm.), von Kupffer (1894) and Stúdnicka (1912) described a lens vesicle lying underneath the single layered ectoderm and completely separate from the optic vesicle (Figs. 272 and 273), while Carrière (1885) in a more mature larva (30 mm.) described a lens, at this stage still vesicular, invaginated within the optic vesicle. Eventually the lens becomes solid, the anterior and vitreous

Figs. 272 and 273.—The Ammocœte Eye (after Stúdnicka).

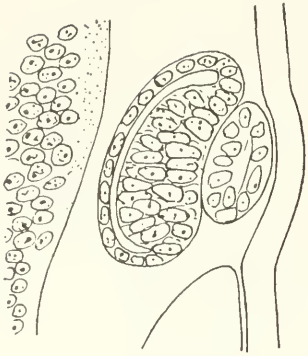

Fig. 272.—The eye of the 8 mm. larva of *Petromyzon*, showing the optic vesicle and the smaller lens vesicle superficial to it.

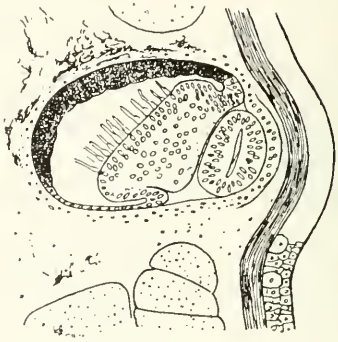

Fig. 273.—The eye of the 18 mm. ammocœtes showing the lens vesicle incorporated into the optic vesicle. In the latter the outer pigmented layer and the highly differentiated inner layer with the projecting visual cells are evident.

chambers fill with fibrillar material, the cornea is entirely cellular, the retina becomes relatively differentiated but blood vessels and mesodermal elements do not invade the vesicular eye (Mawas and Magitot, 1912; Dücker, 1924) (Figs. 274 and 275). Meantime the eye sinks beneath the skin to become separated from it by a considerable thickness of tissue.

The depth at which the vesicular eye lies at this stage beneath the skin suggested to Hagedoorn (1930) that the lens was derived from the retinal

Fig. 274.—The Eye of the Ammocœtes.

[illegible] a late stage. On top is the surface epithelium, underneath which lies the [illegible]odermal skin. Underneath this is the scleral cornea. The lens is full[illegible]med, as also are the anterior and vitreous chambers (a drawing from Maw[illegible]

vesicle ; the suggestion that the eye of the lamprey differed from all other vertebrate eyes in that its elements were all autonomous in the sense that the entire organ arose from the neural ectoderm is, however, by no means proven by the evidence submitted by this author and should be discarded. It is apposite that in the still more primitive eye of the myxinoid, *Bdellostoma*, Stockard (1907) found that the lens appeared in the usual vertebrate way as a vesicle from the surface epithelium independently of the optic vesicle.

LIGHT-SENSITIVE CELLS. In the epidermis of the tail of the ammocœtes there are numerous interesting cells copiously innervated from the lateral line. Morphologically they resemble the apolar visual cells seen in the earthworm or

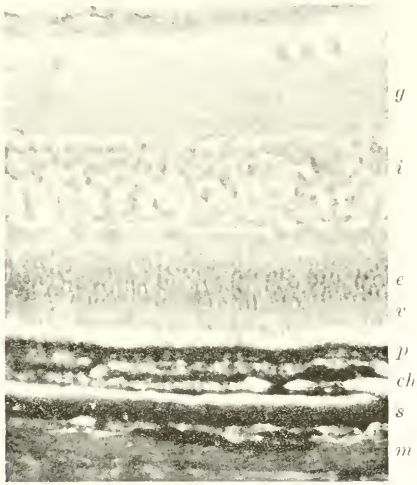

FIG. 275.—SECTION THROUGH THE POSTERIOR SEGMENT OF THE EYE OF THE FULLY DEVELOPED AMMOCŒTES.

g, ganglion cells ; *i*, internal nuclear layer ; *e*, external nuclear layer ; *v*, visual cells ; *p*, pigmented epithelium ; *ch*, choroid ; *s*, sclera ; *m*, muscular tissue (Azan, × 250) (Katharine Tansley).

Mya (Fig. 86) and are said to be associated with a photosensitive pigment ; they probably act as primitive photoreceptors determining phototactic activity (Young, 1935 ; Steven, 1950–51). It will be remembered that light-sensitive cells of the type characteristic of Invertebrates are also found among Chordates in *Amphioxus* as the cells of Joseph[1] ; and it is interesting that the only other Vertebrate which shows evidence of a similar primitive phototaxis is the cave-dwelling salamander, *Proteus anguinus* (Hawes, 1946).

THE LAMPREY EYE

The eye of the lamprey and its relatives is of unusual interest in that it shows a number of primitive characteristics differentiating it clearly from the eyes of Fishes and all other higher Vertebrates ; nevertheless, it conforms closely to the essential structure of the eyes

[1] p. 229.

FIGS. 276 AND 277.—THE EYE OF *LAMPETRA PLANERI*.

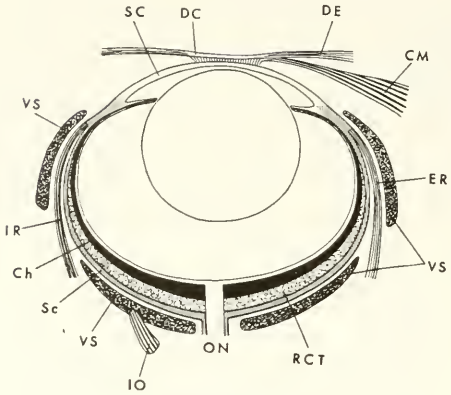

FIG. 276.

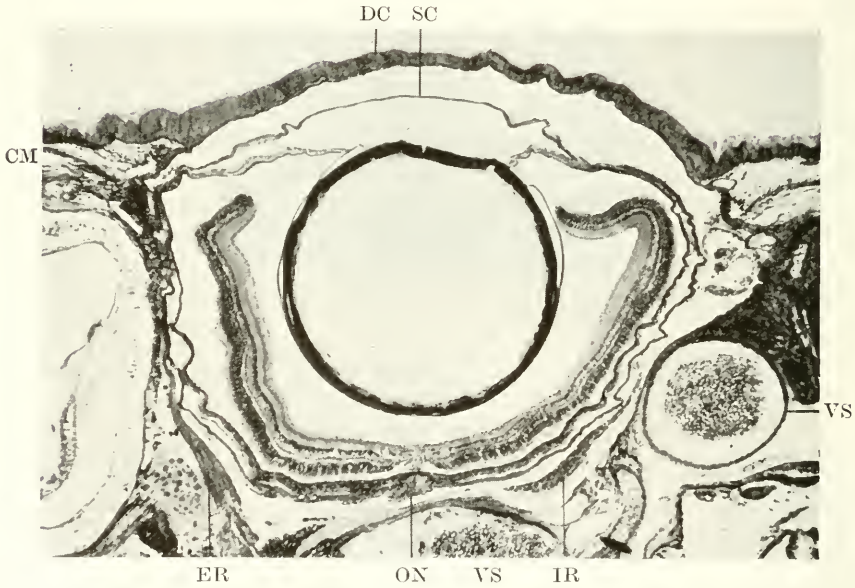

FIG. 277.

The outline of the large circular lens is seen as a dark circle ; it has slipped backwards and the inner part of the lens has fallen out of the section (Mallory's phospho-tungstic acid hæmatoxylin (× 34) (Katharine Tansley).

Ch, choroid (black) ; CM, cornealis muscle ; DC, dermal cornea ; DE, dermal epithelium ; ER, external rectus ; IO, inferior oblique ; IR, internal rectus ; ON, optic nerve ; RCT, retrochoroidal tissue ; Sc, sclera ; SC, scleral cornea ; VS, venous sinuses.

of this phylum. Of all vertebrate eyes it is the simplest (Figs. 276 and 277). Its characteristic features are :

an avascular retina wherein the ganglion cell layer merges with the inner nuclear layer ;
the embryonic nature of the optic nerve, without septa but with an ependymal axis, and provided with non-myelinated nerve fibres ;
the thick epichoroid in certain species ;
the large primitive lens lacking sutures ;
the absence of intra-ocular musculature ;
the separation of the cornea from the surface ectoderm ;
the absence, alone among Vertebrates, of a cartilaginous or bony orbit ;
the blending of some of the extra-ocular muscles ;
and the presence of an extra-ocular muscle of accommodation which acts by deforming the eyeball from the outside.

The structure of the eyes of all adult lampreys (*Petromyzon marinus*, *Lampetra fluviatilis*, etc.) conforms to the same general plan (W. Müller, 1875 ; Franz, 1932–34 ; Walls, 1935–42 ; Rochon-Duvigneaud, 1943 ; Henckel, 1944—*Mordacia*).

THE GLOBE, as in most Fishes, is flattened antero-posteriorly, giving the eye an ellipsoid configuration, the most prominent feature being the large anteriorly-situated lens which makes underwater focusing possible.[1] The *cornea-sclera* is primitive ; the latter is a thin, purely fibrous structure, the former a tenuous lamellated stratum almost reduced to Descemet's membrane together with its endothelium, continuous with the sclera. Superficial to this the skin is transparent and thin, forming a layer in which the dermal glands and vessels are lost and merely the multi-stratified epithelium remains, consisting of 6 or 7 layers of regularly arranged cells. The space between the two structures—the *dermal cornea* and *scleral cornea*—is occupied by a delicate mucoid tissue derived from orbital connective tissue, the loose structure of which allows the globe to rotate freely underneath the skin.

The composite "cornea" of Cyclostomes thus represents an early stage in the development of the typical vertebrate cornea wherein the superficial layers derived from the surface ectoderm have not yet fused with the deeper layers of mesodermal origin. The eye is thus entirely a subcutaneous organ. To the specialized area of transparent skin constituting the dermal cornea, German authors have given the name of PRIMARY SPECTACLE ("primäre Brille"), the term denoting *a fixed transparent structure separate from the globe underneath which the eye is free to rotate* (Fig. 278) (Haller, 1768 ; Treviranus, 1820 ; and others ; and Franz, 1934). Such an arrangement is seen in tadpoles and adult aquatic Amphibians as well as in Cyclostomes. A secondary splitting of the cornea into

[1] p. 276.

two layers to produce a similar configuration may occur in some fishes as an adaptation to protect the eye when the animal is crawling in mud or sand (bottom-fishes, lung-fishes, cat-fishes) or to prevent desiccation in forms which leave the water for air (lung-fishes, eels, mud-skippers, some gobies, etc.). An entirely different configuration—the SECONDARY SPECTACLE—is *formed by the development of a transparent area in the lids,* either a transparent window in a moveable lower lid, as in a few chelonians and some lizards, or by the edge-to-edge fusion of the two lids which have become transparent to form a fixed spectacle as is seen among Fishes in anchovies and in many Reptiles (snakes and some lizards) ; it is this that gives the characteristic glassy stare to the eyes of snakes and most lizards. In this case the cornea is comprised of all its constituent layers and between it and the fused lids there is a true cavity

FIGS. 278 AND 279.—" SPECTACLES."

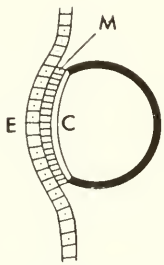

FIG. 278.—The primary spectacle of Cyclostomes and aquatic Amphibians.

E, the surface epithelium forming the dermal cornea ; C, scleral cornea ; M, mucoid tissue between the two.

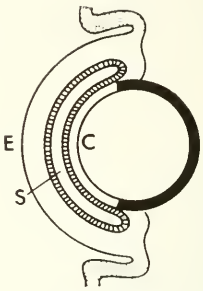

FIG. 279.—The secondary spectacle as seen particularly in Reptiles.

E, the " spectacle " formed by fusion of the lids which are transparent; C, the cornea ; S, the conjunctival sac lined throughout by epithelium, proximally corneal and distally palpebral.

(the conjunctival space) lined by epithelium, the distal part of which represents the palpebral conjunctiva, the proximal the corneal epithelium (Figs. 279 and 470) (Hein, 1913 ; Franz, 1934 ; Walls, 1942).

The *uveal tract* of the lamprey is also primitive in its characteristics. A single artery penetrates the sclera beneath the optic nerve, which divides into four vessels, one for each quadrant ; these break up into a choriocapillaris overlying the retina, but instead of the efferent blood being drained away by veins, the outer half of the choroid is composed of a continuous lake of blood (the SUBSCLERAL SINUS) which in turn leads by four apertures traversing the sclera into a complex system of extra-ocular venous sinuses surrounding the outer aspect of the sclera (Figs. 276–7). In the posterior half of the globe between the subscleral venous sinus and the sclera there is in some species (*Petromyzon marinus*) a peculiar epichoroidal tissue composed of large pigmented

cells and equally large vesicular cells forming a relatively thick cushion between the choroid and the sclera. There is no ciliary body,[1] only a flat ciliary zone, and the immobile non-muscular iris consists merely of the usual two layers of (retinal) epithelium covered anteriorly by a tenuous and lightly pigmented stroma binding together the blood-vessels which are supplied by three anterior ciliary arteries. Contrary to the arrangement in higher Vertebrates, the epithelial layers of the iris continue forwards the state of pigmentation of the corresponding retinal layers ; the anterior layer is pigmented, the posterior unpigmented almost up to the pupillary border. The anterior surface of the iris has a light metallic sheen due to a fine ARGENTEA comprised of a layer of closely packed cells containing guanine crystals, a configuration which is not continued into the choroid.

The angle of the anterior chamber is constructed on simple lines. A ring of large endothelial cells encircles the periphery of the cornea as the ANNULAR LIGAMENT, continues anteriorly with the corneal endothelium and sends strands posteriorly to the choroid suggestive of the tensor choroideæ of Teleosteans ; while from the region of this ring, fine strands span the angle to reach the anterior surface of the iris, reminiscent of a pectinate ligament. The large and almost circular lens is wedged in the immobile pupil and approximates the cornea, separated from it at most by a capillary space ; it is held in place by the support of the cornea in front and the vitreous behind. The lens is primitive in formation compared with the structures found in other Vertebrates, showing a central zone of polygonal or rounded fibres and a somewhat irregular arrangement in the periphery without

[1] The origin of the aqueous humour of Cyclostomes and Fishes is obscure, but it is possible that the ocular fluids are maintained directly by osmosis through the cornea, the pressure being equilibrated through the blood-stream. In fresh-water fish and the lamprey the blood is hypertonic to the medium so that the body fluids are constantly replenished by the absorption of water through the skin by osmosis, the fish excreting the large quantities of fluid thus absorbed by producing immense quantities of urine. In marine teleosts, on the other hand, the blood is hypotonic to the sea-water ; dehydration is avoided only by the copious drinking of the latter. This is actively absorbed in the gut against the osmotic gradient while the excess of salts is excreted differentially in the gut, kidneys and gills. Selachian fishes maintain a high level of urea in the blood (some 2%) thus keeping it at a higher osmotic level than sea-water ; the latter is thus absorbed osmotically while the excess of salts is excreted through the gills. It would appear that *Myxine* has a salt concentration in the blood approaching that of sea-water and thus higher than that of any other vertebrate (Robertson, 1957). It is probable that the fluid-exchange and the pressure equilibrium in the eye is maintained in much the same manner. There would seem to be no anatomical basis in any cyclostome or fish for an elaborate secretory mechanism for the intra-ocular fluid ; the only types which possess ciliary processes are the Selachians and these, in Franz's view (1934), probably serve merely as a mechanism for supporting the lens. All land animals, on the other hand, secrete the aqueous humour. It should not be considered strange that the tissues of the earliest Vertebrates (fresh-water agnathous fishes) were hypertonic to the medium in which they lived ; the same relationship is seen in the tissue-cells of man which are maintained in a state of hypertonicity in comparison with the surrounding tissue-fluid by an osmo-regulation depending on respiratory activity (see Bartley, Davies and Krebs, *Proc. roy. Soc. B.*, **142**, 187, 1954).

sutures (Capraro, 1934–37).[1] It has a light yellow coloration derived from a pigment the composition of which is unknown (Plate, 1924 ; Franz, 1932 ; Walls and Judd, 1933).

The *retina*, even at this early stage of Vertebrate evolution, shows the essential architecture of the vertebrate eye ; but is entirely avascular and without any suggestion of an area centralis (Fig. 280). Next to the outer layer of pigmentary epithelium lie the visual elements,

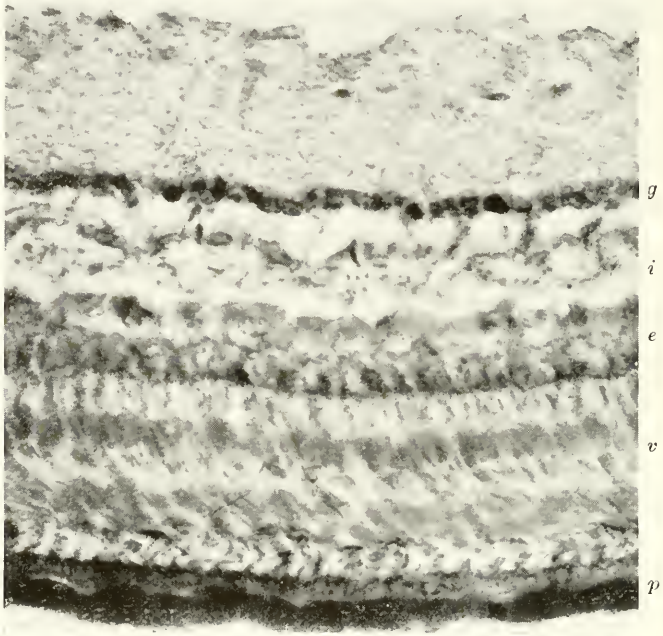

Fig. 280.—The Retina of *Lampetra fluviatilis*.

g, ganglion cells ; *i*, internal nuclear layer, consisting essentially of horizontal cells above and bipolar cells below ; *e*, external nuclear layer ; *v*, visual cells ; *p*, pigmented epithelium (Feulgen, × 370) (Katharine Tansley).

thereafter their nuclei form an outer nuclear layer which is followed by a combined layer containing bipolar cells, horizontal cells, amacrine cells and a few sparse ganglion cells.

The nature of the *visual elements* has given rise to some controversy, but most authorities are now agreed that even in this, the most primitive of Vertebrates, two types of cell exist, a relatively long and a relatively short cell, the former with a voluminous ellipsoid and short external segment, the latter with a smaller ellipsoid capped by a longer external segment. The differentiation between the two types and their relative numbers vary in different families (Walls, 1935). In the primitive

[1] Compare the lens of lizards, p. 361.

genus, *Ichthyomyzon*, the two differ little in size ; in *Lampetra fluviatilis* the difference is marked and in *Entosphenus* it is maximal. In shallow-water forms such as *Lampetra fluviatilis* and the brook lampreys, the two types are found in approximately equal numbers, while in those which live in deeper waters (*Petromyzon marinus*, etc.) and presumably demand greater sensitivity to light, the short greatly outnumber the long (Figs. 281 and 282).

The existence of a duplex mechanism in the retina has not always been accepted and the nature of the cells has long been called in question. Heinrich Müller (1857) who first studied the subject in *L. fluviatilis*, differentiated the

Fig. 281.—The Visual Cells of the Atlantic Lamprey, *Petromyzon marinus*.

Showing the "long" and the "short" elements (× 1,000) (Gordon Walls).

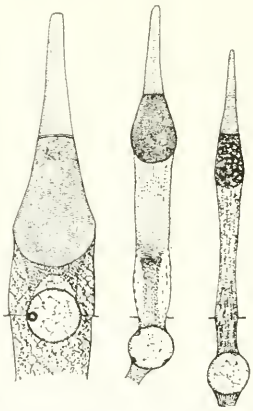

Fig. 282.—The Visual Cells of the New Zealand Lamprey, *Geotria australis*.

There are three types of cell in approximately equal numbers, one plump (to the left), one slender (to the right) and an intermediate type (middle) with a eosinophobic ellipsoid (× 1,000) (Gordon Walls).

two types of cell, and while initially he called them both cones, he later (1862) suggested that the short elements were rods. Since his time every possible suggestion has been made—that both cell-types are rods (Schultze, 1866–71 ; Franz, 1932) ; that both are cones (Kohl, 1892) ; that the cells are neither rods nor cones but primitive and undifferentiated in type (Plate, 1924 ; Dücker, 1924); that the long cells are cones and the short rods (Walls, 1935); or—the view of the majority of workers—that the long cell is a rod and the short a cone (W. Krause, 1868–76 ; Langerhans, 1873–76 ; Greeff, 1900 ; Tretjakoff, 1916 ; R. Krause, 1923). Most of the evidence brought forward in support of these divergent views is morphological in nature—a somewhat dangerous basis for the differentiation of rods and cones.[1] The demonstration by Kühne (1878) that rhodopsin is present in the retina of the lamprey proves the presence of rods ; the difference in the two types of cell suggests strongly a duplex population;

[1] p. 251.

but the presence of a dendritic foot-piece in the long cells and a smooth knob in the short (Tretjakoff, 1916) as well as the comparative and taxonomic evidence collected by Walls (1935), provide weighty evidence in favour of Heinrich Müller's original suggestion that, despite their length, the long elements are probably cones and the short, rods. At the present time, as was suggested by W. Müller (1875) and maintained by Franz (1934), it may be safer, while admitting the presence of two morphologically different types of cell, to refrain from dogmatic differentiation until more conclusive evidence derived from their histochemistry or neural connections is available.

The *optic nerve* is primitive, consisting (unlike that of Fishes) of non-myelinated fibres (Bruesch and Arey, 1942) ; as occurs in the human embryo there is no septal system but merely an axial column

FIGS. 283 AND 284.—THE OPTIC NERVE OF CYCLOSTOMES.

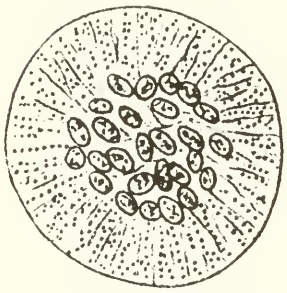

FIG. 283.—The optic nerve of the ammocœte larva (after Stúdnicka).

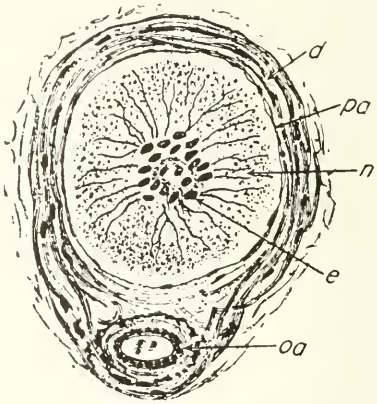

FIG. 284.—The optic nerve of *Lampetra fluviatilis* (after Dücker).

In both cases there is no septal system but merely an axial column of ependymal cells running down the centre of the nerve sending processes radiating to the surface.

d, dural sheath ; *pa*, pia arachnoid sheath ; *n*, nerve fibres ; *e*, ependymal cells sending out radiating processes ; *oa*, ophthalmic artery.

of cell-bodies, probably ependymal in nature, running down the nerve, each sending processes radiating to the surface forming a primitive oligodendroglial system (Deyl, 1895 ; Stúdnicka, 1912 ; Keibel, 1928 ; Walls, 1942 ; Prince, 1955) (Figs. 283 and 284). The chiasma remains within the brain and in it the optic nerves cross as separate individuals without division into fascicles or bundles.

THE EXTRA-OCULAR STRUCTURES of the eye of the lamprey are simple. Contrary to the configuration found in all other Vertebrates, there is no skeletal orbit, but the organ lies in a simple connective-tissue capsule. The orbits and the eyes are laterally placed so that no

binocular field is possible. The rectus muscles are largely blended together and are inserted into the globe as a ring around the periphery of the cornea ; the inferior oblique arises in common with the internal rectus, and the superior oblique, identifiable only by its nerve-supply, is inserted into the infero-temporal quadrant of the globe. The nerve-supply to the muscles corresponds to the scheme common to all Vertebrates (including man) except that the sixth cranial nerve appears to supply the inferior as well as the external rectus ; it may be, however, that the trunk contains fibres derived from the third nucleus. The most interesting feature, however, is the CORNEALIS MUSCLE, a

FIG. 285.—THE CORNEALIS MUSCLE OF THE LAMPREY.

The cornealis muscle, *c*, running horizontally outside the orbit on the caudal aspect of the globe, showing its insertion into the cornea (Mallory's phospho-tungstic acid hæmatoxylin) (× 44) (Katharine Tansley) (cf. Fig. 276).

massive muscle arising outside the orbit on the caudal aspect and inserting into the transparent dermal cornea (Tretjakoff, 1916) (Fig. 285) ; its function is accommodative, drawing this element of the cornea taut and, in so doing, flattening the scleral cornea, pressing the lens backwards towards the retina and thus rendering the normally myopic eye (—8 dioptres) emmetropic or even hypermetropic. Unlike man, the lamprey thus accommodates for distant vision.[1] An accommodative mechanism acting by deforming the globe from the outside is among Vertebrates unique to the lamprey.

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