

## CHAPTER IX

### THE EVOLUTION OF THE VERTEBRATE EYE

SIR EDWIN RAY LANKESTER (1847–1929) (Fig. 240), one of the foremost British naturalists of the last generation, made outstanding contributions to the subject-matter of this chapter. The origin of the vertebrate eye has long been a puzzle and indeed still is ; and Lankester was one of the first to introduce rationalism into the problem which had been largely speculative up to his time. He suggested that in the early Proto-chordates, transparent marine animals, an eye associated with the central nervous system would be a more plastic organ than one derived from the integumentary epithelium and as effective optically in organisms of this type ; as the bodies of Vertebrates become opaque, migration of the eye towards the surface became an obvious evolutionary expedient. He was an example of that erudite type of scientist who was yet able to popularize his philosophy, a type in which Britain has always been rich. His academic career was full—Professor of Zoology and Comparative Anatomy at University College London (1874–90), Linacre Professor of Comparative Anatomy at Oxford (1891–98), director of the Natural History Department of the British Museum (1898–1907), and much of that time Fullerian Professor of Physiology and Comparative Anatomy at the Royal Institution, London. He founded the Marine Biological Association in 1884, was its President in 1892, and received the Royal (1885) and Copley (1913) Medals of the Royal Society.

The VERTEBRATE PHYLUM is of enormous antiquity and stems from the primitive Agnatha, jaw-less pre-fishes, the fossil remnants of which are 400 million years old and are found abundantly in ancient Silurian rocks. Their ancestors are unknown<sup>1</sup> but their descendants have become the lords of the earth. It is interesting that as a general rule evolution proceeds through primitive forms which, because of their simplicity and plasticity, have the potentiality to evolve into more highly differentiated forms ; but these latter, because of their high differentiation and consequent superior equipment, can exterminate their primitive forebears in the struggle for existence, but for the same reason are incapable of further differentiation. The tendency is therefore for evolution to proceed from primitive forms which have become largely extinct, producing in its progress a series of evolutionary dead-ends each showing different highly developed types of adaptive mechanisms designed to meet different specialized circumstances.

During recent years the views of zoologists on evolution within the vertebrate phylum have changed considerably and it is probable that they have not yet finally crystallized (Romer, 1947 ; Trewavas *et al.*, 1955) (Fig. 241). It would seem established, however, that the most archaic vertebrates are the worm-like Agnatha, pre-fishes without jaws or limbs, which survive to-day in the primitive

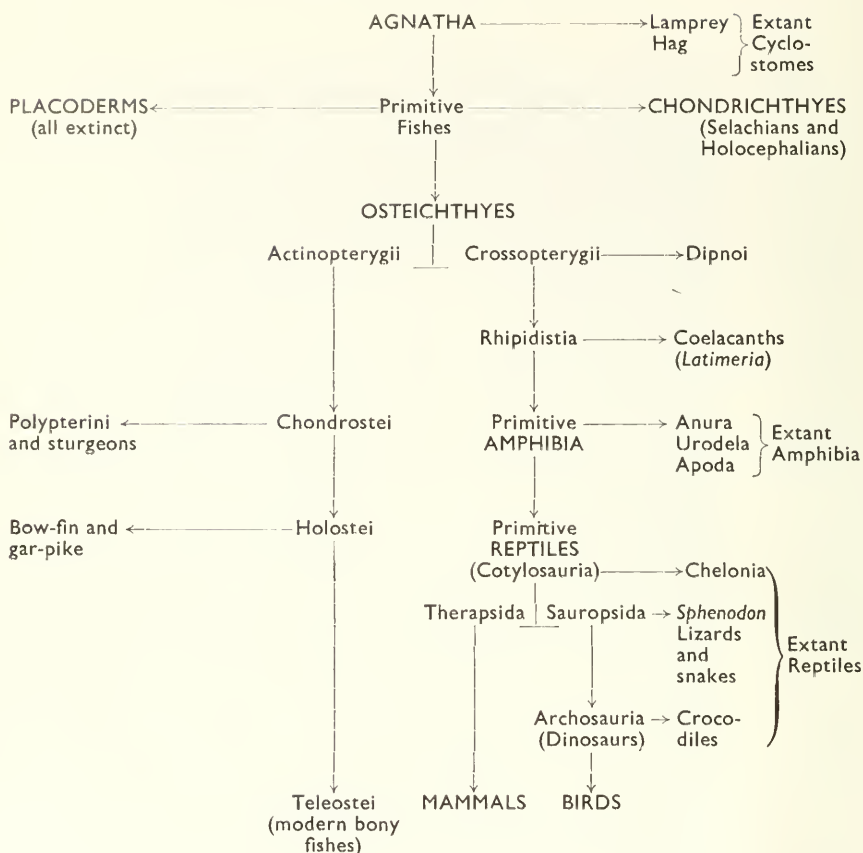
<sup>1</sup> At one time or another the ancestry of Vertebrates has been sought in almost every invertebrate group, particularly annelid worms, Arthropods (especially Arachnids through Eurypterids). Perhaps the most reasonable theory, however, ascribes a common origin to the larvæ of the simplest Chordates and those of Echinoderms, despite the vast and obvious discrepancy between the adults in each phylum. Palæontology, however, provides no record of such tiny, soft-bodied creatures as these larvæ since they are incapable of preservation as fossils (see Romer, 1947).



FIG. 240.—SIR EDWIN RAY LANKESTER (1847–1929).  
(From a portrait by John Collier in the Linnean Society.)

## THE EYE IN EVOLUTION

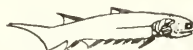
FIG. 241.—THE VERTEBRATE PHYLUM



EXTINCT VERTEBRATES  
(Drawn not to scale but to standard size)



Agnathous Fishes

*Pteraspis**Cephalaspis*

Placoderm



Rhipidistian

Primitive  
AmphibianPrimitive  
ReptileDinosaur,  
*Diplodocus*

Therapsidan

Cyclostomes, the lamprey and the hag. From these there evolved somewhere in the Upper Silurian period, 350 million years ago,<sup>1</sup> the true (gnathous) fishes, possessed of jaws and paired fins. From these primitive fishes three classes radiated : (1) the Placoderms, a motley class mostly with bony armour, which flourished in Devonian times but none of which survived the Palæozoic era ; (2) the Chondrichthyes, a class of cartilaginous fishes of great age which are now represented only by the Selachians (sharks and rays) and Holocephalians (deep-sea chimeras) ; and (3) the Osteichthyes, the much larger class of bony fishes. While the Placoderms have disappeared, and the cartilaginous fishes, prolific in the older geological periods, have steadily decreased in importance in more recent times, the bony fishes have shown themselves remarkably adaptive. By the end of the Palæozoic era they had attained almost sole possession of fresh-water streams and lakes ; at that time they had invaded the seas also and rapidly constituted the vast majority of marine forms.

These bony fishes may be divided into two main sub-groups, each of which has numerous survivors : the Actinopterygii and the Crossopterygii. From the former a series of forms arose in linear progression—the Chondrostei, still with a largely cartilaginous internal skeleton, degenerative representatives of which still survive as the Polypterini (two species of which are extant) and the sturgeons ; the Holostei, provided with bony skeletons, represented today only by two American fresh-water fishes, the bow-fin and the gar-pike ; and eventually the Teleostei, the most specialized of all fishes which include practically all modern species.

From the early Crossopterygii the Dipnoi (lung-fishes) appeared as an aberrant off-shoot in the lower Devonian period ; of these, three species survive today, swamp-dwelling, mud-loving and eventually air-breathing fishes in which the swim-bladder has been retained as a functioning lung. From the main group, however, a direct line of vertebrate descent continued through the Rhipidistia (a derivative of which exists today as the *Coelacanth*, *Latimeria*) ; these fish could already breathe air so that they only had to turn their fins into legs and modify the ear to become *Amphibia* and survive on land. Developing as tadpole-like aquatic creatures, they underwent this remarkable metamorphosis as they matured into their adult forms. Initially they lived side-by-side with their cousins, the lung-fishes, in the swamps ; but when the great droughts appeared and the fresh-water pools dried up towards the end of the Devonian period some 300 million years ago, the lung-fishes largely perished, but the *Amphibians*, capable of creeping and feeding on land, survived. Their first representatives have long become extinct and the class survives today only in three relatively unimportant and highly specialized groups—the frogs and toads (*Anura*), the salamanders and newts (*Urodela*) and the worm-like *Cæcilians* (*Apoda*). From the highly adaptable primitive types, however, there evolved in the Upper Carboniferous period the first fully terrestrial vertebrates, the most primitive *Reptiles*, born on land and capable of existing away from water altogether. This spectacular step in evolution was made possible by the development of a large and highly nutrient egg protected by a porous shell so that the young reptile could emerge fully equipped for terrestrial life.

For many millions of years these primitive reptiles flourished exceedingly ; emerging on to the hitherto unexploited land, rich in vegetation and food, they spread and gave rise to a multitude of new types, some of them of incredible form and giant size. They still retained, however, the cold-blooded characteristic of their fish and amphibian ancestors, and thus, presumably owing to the climatic changes at the end of the Mesozoic era, this group which had dominated the

<sup>1</sup> See p. 754.

earth for more than 100 million years perished, apart from a few unimportant exceptions—the very primitive Chelonians (tortoises and turtles), the almost extinct Rhynchocephalian, *Sphenodon*, of lineage almost as remote; and the more modern groups, lizards and snakes and crocodiles.

The handicap of cold-bloodedness limited these surviving Reptiles to the warmer parts of the earth. In the even temperature of the sea the Teleosteans could flourish without hindrance; to populate the cooling earth homeostasis had to be achieved; this was eventually acquired by Birds and Mammals, the former assuming an insulating coat of feathers, the latter usually of hair in place of the scales characteristic of Reptiles. Of the two the Mammals claim the more primitive descent, stemming from the Therapsidans, mammalian-like Reptiles which flourished in Permian and early Triassic times. During the latter period it would seem that Mammals made their appearance as small mouse-sized creatures, but throughout the entire Mesozoic era they appear to have been sparse, leaving few fossil remains; it was not until the end of the Cretaceous period, 75 million years ago, when the great carnivorous Reptiles finally died off that these retiring, inconspicuous creatures, probably nocturnal or arboreal in habit, were able to take the leading place in evolutionary progress. This they have done to such good purpose that they have adapted themselves to and become completely predominant in almost every environment on land, some of them even returning to the water wherein their lately acquired superiority afforded them a relatively easy existence (whales, seals, Sirenians) while others (bats) have invaded the air.

Parallel with the Therapsida stands the other reptilian group of Sauropsida, of which lizards and snakes are a direct off-shoot; from it was derived the Archosauria, a group characterized by a limb-and-girdle structure enabling them to run semi-erect upon their hind legs with a bipedal gait. The only members of this stock which have survived are the crocodiles and their relatives the alligators; but, particularly in their most spectacular forms, the Dinosaurs, some of them as heavy as 40 or 50 tons, they constituted the dominant terrestrial type during the latter half of the Mesozoic era. From these are descended modern Birds which show innumerable reptilian features.

Curiously it was from the most primitive type of placental Mammal, the Insectivores, that the Primates and Man evolved, and in the evolution of these the great advance has been associated with the brain. This was achieved in a peculiar way. A small and unimportant group became adapted to arboreal life, thus developing their cortical capacity by the coordination of the eye and hand; thereafter, descending from the trees and freeing their hands by becoming bipedal, they passed the critical point at which physical dexterity could combine with conceptual thought and the faculty of speech, and thus a new method of evolution became possible based on the transmission of cultural experience. At this stage the potentialities of vision are measured not by the optical and structural excellence of the receptive end-organ, but by the apperceptive capacity of the mind. In this way, just as the Mammals defeated the lower Vertebrates on land, leaving the water to the Teleosts and the air to the Birds, so the Placentals eliminated the Monotremes and Marsupials wherever they came in contact with them, the Carnivora dominated the lower Placentals, the monkeys the Prosimians, and finally Man triumphed over all the others.

From the anatomical point of view—and certainly from the aspect of the structure of the eye—these six classes of the Vertebrates, neglecting the Cyclostomes, can conveniently be reduced to three great groups as suggested by Huxley:



1. The *ICHTHYOPSIDA*—Fishes and Amphibians, the primary habitat of which is water—completely so in the case of the first and developmentally so in the second. Although the eyes of adult Amphibians show many terrestrial adaptations, the larval stage is spent in water and the adjustments for aerial vision are added to the general plan of the aquatic eye.

2. The *SAUROPSIDA*—Reptiles and Birds which, despite the difference in their external appearance, show many close structural affinities. In them the eyes have become completely adapted to aerial vision.

3. The *MAMMALIA*, in which the eye, starting from a primitive reptilian source, has developed along separate lines adapting itself to almost every environmental habitat—including a return to aquatic vision.

#### THE PHYLOGENY OF THE VERTEBRATE EYE

We have already seen that the eyes of Invertebrates are developed from the surface ectoderm and that the visual cells are connected to the nervous system secondarily; the eyes of Vertebrates, on the other hand, arise from the neural ectoderm. It is true that the neural ectoderm itself is ultimately derived as an infolding from the surface layer, but the *CEREBRAL EYE* of Vertebrates indicates a major evolutionary step affording the sentient layer of cells all the opportunities for the pluripotential differentiation characteristic of the central nervous system of which in every sense it forms an integral part. An apparatus capable of subserving a highly developed sense of vision depends no less on the efficiency of its central nervous representation which interprets its images than on the peripheral sensory apparatus which receives and resolves them. Moreover, an endoneural receptor immune because of its position to other stimuli, mechanical or chemical, can evolve a delicacy of response without danger of false alarms that could not be attained by an organ exposed on the surface. The significance of the origin of the vertebrate eye is thus apparent; the process is essentially the same as in Invertebrates, both the eye and the central nervous system being ectodermal, but in the latter the eye has evolved from the surface ectoderm primarily, in Vertebrates it is secondarily derived.<sup>1</sup>

The curious thing, however, about the evolution of the vertebrate eye is the apparent suddenness of its appearance and the elaboration of its structures in its earliest known stages. There is no long evolutionary story as we have seen among invertebrate eyes whereby an intracellular organelle passes into a unicellular and then a multicellular eye, attaining by trial and error along different routes an ever-increasing degree of complexity. Within the vertebrate phylum the eye shows no progress of increasing differentiation and perfection as is seen in the brain, the

<sup>1</sup> It is to be noted that the sensory cells in the epidermis of the tail of the ammocete larva of the lamprey are probably light-sensitive (Steven, 1950-51); they resemble the apolar light cells seen in some worms (*Lumbricus*) and molluscs (*Mya*) (p. 131). This is the only instance of the occurrence among Vertebrates of the primitive light cells characteristic of Invertebrates, and is analogous (perhaps) with the cells of Joseph seen in the integument of *Amphioxus* (p. 229).

ear, the heart and most other organs. In its essentials the eye of a fish is as complex and fully developed as that of a bird or man; the differences between the members of the series are relatively minor in character, adaptations to the habits of the animals rather than expressions of phylogenetic evolution. All Vertebrates have a three-layered retina and a pigmentary epithelium, all have the same dioptric apparatus of a cornea and an epithelial lens, all have the same nutrient mechanism. It is true that the essential visual components except the three-layered retina are found in many invertebrate eyes; but at the same time it is to be remembered that the optic ganglion of the latter group corresponds essentially to the nervous layers of the retina of Vertebrates. Despite these similarities, however, a revolution has taken place.

Throughout the whole phylum paired lateral eyes are present, although occasionally, as in specialized predators such as the hagfish, *Myxine*, or in cave-dwelling or abyssal fishes, subterranean amphibians and reptiles and the mole, they may degenerate.<sup>1</sup> In the most primitive vertebrates known to man—the long extinct agnathous fishes (*Pteraspis*, *Cephalaspis*, etc.) the fossil remnants of which are found in the rocks of the Silurian era<sup>2</sup>—a median and two lateral eyes were present. In the extant representatives of this primitive stock, the lampreys (*Petromyzon*), the lateral eyes are rudimentary and hidden in the ammocoete (larval) stage; but in the adult they become well-developed and reach the surface (Figs. 276–7), while the animal is also provided with median pineal and parietal “eyes”.<sup>3</sup> Although primitive, however, and lacking the diagnostic characteristics of true fishes, the lateral eyes of this most primitive type emerge as fully differentiated organs and shed little light on the origin of the eyes of the higher species. It would seem, therefore, that the vertebrate eye evolved not as a late off-shoot from the simple eye of Invertebrates after the latter had reached an advanced stage; it probably emerged at a very early stage, further back than geological evidence can take us, and developed along parallel but diverging lines. The apposite remark of the great German anatomist, Froriep (1906), that the vertebrate eye sprang into existence fully-formed, like Athene from the forehead of Zeus, expressed the frustration of the scientists of half a century ago to account for its appearance; today we are little wiser.

The apparently revolutionary changes in morphology which characterize Vertebrates are not, of course, confined to the eyes. The abruptness of the separation between the backboneed and backboneless animals was evident to Aristotle and was firmly drawn by Lamarck in 1809 for the pedigree of the former—presumably from the latter—still remains unknown and all the theories which have been advanced

<sup>1</sup> p. 71.<sup>2</sup> 320 to 350 million years ago, p. 754.<sup>3</sup> p. 713.

are suggestive rather than convincing. Moreover, in the case of a soft organ any help from fossil types is lacking. We are therefore driven to seek what evidence we can from ontogeny.

- Froriep. *Hb. d. vergl. u. exper. Entwicklungslehre d. Wirbeltiere*, Jena, 2 (1906).  
*Anat. Anz.* (Suppl.), 29, 145 (1906).  
 Lamarck. *Zoological Philosophy* (1809).  
 Romer. *Vertebrate Paleontology*, Chicago (1947).  
 Steven. *J. exp. Biol.*, 27, 350 (1950).  
*Quart. J. micr. Sci.*, 92, 233 (1951).  
 Trewavas, White, Marshall and Tucker. *Nature* (Lond.), 176, 126 (1955).

#### THE ONTOGENY OF THE VERTEBRATE EYE

Ontogenetically, the central nervous system first appears as a superficial groove along the mid-dorsal line of the embryo which eventually invaginates,<sup>1</sup> the anterior part to form the anlage of the brain, the remaining and greater part to form the spinal cord. At an early stage before the closing-in process occurs, the anterior cephalic end grows more rapidly than the rest and forms three primary vesicles,<sup>2</sup> and at the cephalic end of the rudiment of the forebrain, tucked into a recess at each corner, a paired lateral depression appears, known as the *optic pits* (*foveolae opticae*). These paired pits, lying on the surface of the open cephalic plate, have been seen on the surface of many types of embryos in some of which they are pigmented (Froriep, 1906; Lange, 1908; Franz, 1934; and others) (Figs. 242 to 247). As the neural groove invaginates to become the neural tube, the optic pits become invaginated with it to form the primary optic vesicles, which, reaching the surface as lateral out-pouchings of the cerebral vesicles, again invaginate to form the secondary optic vesicles (or optic cups).

In all Vertebrates the retina participates in the high degree of differentiation which characterizes the central nervous system. The proximal wall of the optic cup remains as a unicellular layer and acquires pigment to form the pigmentary epithelium, but its inherent plasticity is seen in the capacity of the amphibian epithelium to regenerate an entirely new functional retina if the inner layer is removed (Stone, 1950). The neuro-epithelium which forms the distal layer of the cup, like that which determines the cerebral and cerebellar cortex, differentiates into three strata—a marginal zone of ganglion cells, an intermediate mantle zone (bipolar, amacrine, horizontal and

<sup>1</sup> The fact that the nerve-cord in *Amphioxus* first appears as a solid rod which canalizes at a later stage has suggested to some authorities that this sequence represents a phylogenetic step in the evolution of the central nervous system of Vertebrates; but it is to be remembered that the evidence indicates that the Lancelets are an off-shoot of the main vertebrate stock rather than a primitive type. It is also to be noted that Graham Kerr (1919) described the forebrain of *Lepidosiren* and other fishes as developing in the form of a solid rod from which the optic vesicles grew as solid buds to become canalized later. This, however, is probably merely a question of the timing of various stages of development; and no dogmatic judgment on this question can yet be given.

<sup>2</sup> p. 532.



## THE EYE IN EVOLUTION

FIGS. 242 TO 247.—THE ONTOGENETIC DEVELOPMENT OF THE LATERAL EYE OF VERTEBRATES.

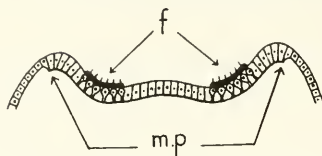


FIG. 242.

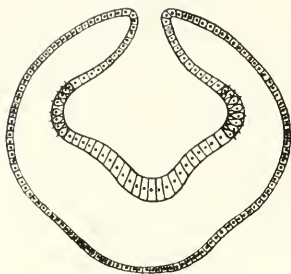


FIG. 243.



FIG. 244.

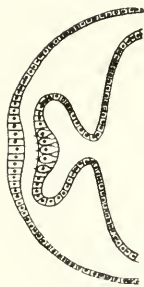


FIG. 245.

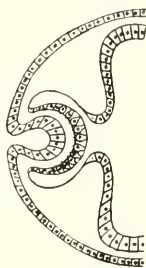


FIG. 246.

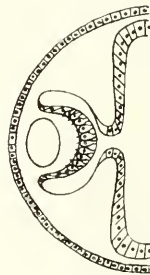


FIG. 247.

FIG. 242.—The appearance of the foveolæ opticae (*f*) on the dorsal ectoderm of the cephalic (medullary) plate (*m.p.*).

FIG. 243.—Invagination of the surface ectoderm with the optical area to form the primitive neural tube.

FIG. 244.—Evagination of the primary optic vesicle.

FIG. 245.—The commencement of secondary invagination of the neural epithelium with thickening of the surface epithelium.

FIG. 246.—Invagination of the surface epithelium.

FIG. 247.—Detachment of the lens from the surface epithelium.

Müller's cells) and an outer zone of sensory cells, perhaps the linear descendants of the ependymal cells (rods and cones). In this way the stratification of cells with their accompanying system of interconnecting neurones allows the appearance of a complex conducting and associating apparatus. With very few exceptions the retina of Invertebrates is

formed by a single ectodermal layer ; but into the retina of Vertebrates is thus aggregated the analogue of the optic ganglion of Invertebrates ; it becomes an island of the central nervous system, and the optic nerve becomes a tract of this system connecting the outlying part with the main body.

In the vast majority of cases we have seen that the receptor end of the sensory cell in the epithelial eye of the Invertebrate lay towards the surface of the body,<sup>1</sup> but when it was enfolded in the neural tube of the Vertebrate, this end now lay deeply and the pole from which the nerve fibre issues became superficial (Fig. 247). It follows that in the cerebral eye of the Vertebrate, light must traverse the whole thickness of the retina in order to reach the sentient layer ; such an arrangement we have already called an INVERTED RETINA in contradistinction to the more primitive VERTED RETINA wherein light first strikes the visual cells before reaching their nervous prolongations.<sup>2</sup> The inverted retina may seem an anomalous arrangement from an optical point of view, but it carries the advantage that the visual receptors can be brought into contact with the pigment and that the part of the retina in which the greatest activity occurs lies nearest the capillaries of the choroid ; both of these—pigment and a dense layer of blood-vessels—for optical reasons could only be situated deeply to the visual elements. Moreover, an inverted arrangement allows the evolution of intracellular colour filters within the visual cells (Walls and Judd, 1933) and permits an increase of the resolving power of the central region by the formation of a fovea (Walls, 1937).

The remainder of the eye is derived from the surrounding ectodermal and mesodermal tissues. The surface ectoderm devotes itself entirely to the formation of the dioptric apparatus, an arrangement which allows greater efficiency than was the case in Invertebrates in which a refringent mechanism was developed from the same layer as the sentient cells themselves. Intercalary cells in the sentient layer, however, retain this function to some extent by secreting a transparent medium (the vitreous). Organs of protection are provided from the surrounding mesodermal tissues—a fibrous sclerotic coat, lids, a lacrimal apparatus, and a bony orbit ; and from the same source a motor apparatus is added, and a vascular system provided.

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| Franz. Bolk's <i>Hb. d. vergl. Anat. d. Wirbeltiere</i> , Berlin, 2 (ii), 989 (1934).      | Lange. <i>Zbl. prakt. Augenheilk.</i> , <b>32</b> , 131 (1908).         |
| Froriep. <i>Hb. d. vergl. u. exper. Entwicklungslehre d. Wirbeltiere</i> , Jena, 2 (1906). | Stone. <i>Anat. Rec.</i> , <b>106</b> , 89 (1950).                      |
| <i>Anat. Anz.</i> (Suppl.), <b>29</b> , 145 (1906).  | Walls. <i>Arch. Ophthal.</i> (Chicago), <b>18</b> , 912 (1937).         |
| Kerr, Graham. <i>Textbook of Embryology</i> , London (1919).                               | Walls and Judd. <i>Brit. J. Ophthal.</i> , <b>17</b> , 641, 705 (1933). |

<sup>1</sup> p. 146.

<sup>2</sup> p. 146.

## THE EMERGENCE OF THE VERTEBRATE EYE

Since Wilhelm Müller (1875) first put forward his view that the pigment-spot in *Amphioxus* represented the forerunner of the vertebrate eye, many hypotheses have been advanced to explain its sudden and peculiar appearance, but even today no theory can be said to be completely convincing and each raises difficulties in interpretation. These theories we shall now briefly discuss.

Ray Lankester (1880-90) was among the first to appreciate the importance of the cerebral origin of the vertebrate eye and reasoned that, with the visual cells buried in the central nervous system, the original pelagic pre-vertebrate must have been transparent, as indeed are Ascidians and Lancelets, so that the light could traverse their bodies. As the body became opaque the eye was then forced to travel nearer and nearer to the surface until eventually it became separated from it only by a layer of ectoderm which retained its primitive transparency. In this view the light-sensitive cells originally associated with the medullary tube migrated to the surface bringing with them their associated pigment cells, and were multiplied and differentiated to form the retina; meantime, the surface epithelium in the corresponding area remained transparent and ultimately became differentiated to form the dioptric apparatus (cornea and lens).

This view seemed a reasonable explanation of the phenomenon and was crystallized by Balfour (1881) who pointed out that although the retina appeared to derive from the brain it did not originate there but, like the photoreceptors of Invertebrates, was really of integumentary origin, appearing initially as patches of photosensory epithelium on the area of the dorsal ectoderm which happened to become involutioned with the neural tube (Figs. 248 to 254). Such a theory accounted for the inversion of the retina as well as its cerebral origin—a characteristic unique among vertebrate sense organs. The concept that the vertebrate eye ultimately derives from the skin was supported by a number of investigators,<sup>1</sup> while Schimkewitsch (1921) carried the theory further by suggesting that the lateral eyes were merely a pair of a series of homologous pit-like sense organs, the more anterior of which were photosensory, a series in which were included other evaginations of the roof of the diencephalon such as the pineal and parietal eyes. In these latter eyes there is no secondary invagination so that a verted retina is formed; and Sleggs (1926) and Estable (1927) explained the secondary invagination of the optic vesicles as a positive evolutionary step taken in order that abundant nourishment might be available from the choroid to allow a high degree of differentiation and activity in the sensory mechanism.<sup>2</sup>

<sup>1</sup> See Kennel (1881), Dohrn (1885), Keibel (1906), Frioriep (1906), Lange (1908), Franz (1910) and others.

<sup>2</sup> p.

The origin of the essential sensory cells, the rods and cones, has long remained a matter of dispute. Ever since the time of Schwalbe (1874) they had been generally considered as neuro-epithelium. Krause (1875), however, originally put forward the suggestion that they

FIGS. 248 TO 254.—HYPOTHETICAL SCHEME FOR THE PHYLOGENETIC DEVELOPMENT OF VERTEBRATE EYES.

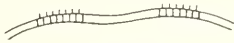


FIG. 248.

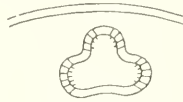


FIG. 252.



FIG. 249.

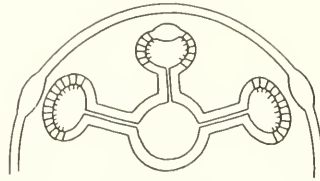


FIG. 253.

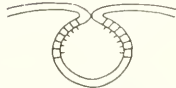


FIG. 250.

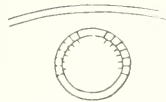


FIG. 251.

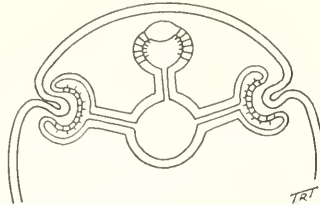


FIG. 254.

FIG. 248.—Photosensitive ciliated ectoderm on the dorsal aspect.

FIGS. 249 and 250.—Invagination of the surface ectoderm to form the neural tube, carrying with it the photosensitive ectoderm.

FIG. 251.—The formation of the neural tube enclosing the photosensitive epithelium as ependyma.

FIG. 252.—Commencing evagination of the neural tube.

FIG. 253.—The formation of one median and two lateral optic vesicles.

FIG. 254.—Invagination of the surface ectoderm with secondary invagination of the lateral optic vesicles to form two lateral eyes with inverted retinae. The surface epithelium takes no part in the development of the median eye which forms its own dioptric apparatus (lens) in the distal part of the vesicle which itself does not undergo secondary invagination and thus forms a verted retina.

were derived from the ciliated ependymal cells lining the neural tube, the cilia eventually forming the outer segments of the visual cells—a view, however, which he quickly withdrew (1876). The vast authority of these two pioneers in the histology of the visual organs long remained unchallenged, but the view that this layer of cells might



be ependymal in origin, the receptor end being phylogenetically homologous with the single cilium of an ependymal cell, was revived by Leboucq (1909), a theory which was elaborated with great persuasiveness by Studnicka (1912-18), and subsequently supported by Walls (1939) and Willmer (1953). In this view the phylogenetic homologue of the vertebrate retina may be assumed to be the infundibular organ of *Amphioxus*<sup>1</sup>; but it must be remembered that any convincing phylogenetic sequence connecting the two is lacking.

FIGS. 255 TO 258.—BOVERI'S CONCEPTION OF THE DEVELOPMENT OF THE VERTEBRATE EYE FROM THE ORGANS OF HESSE OF AN AMPHIOXUS-LIKE ANCESTOR.

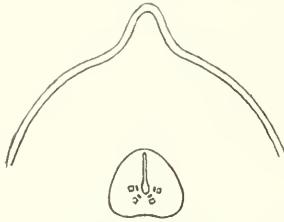


FIG. 255.—Symmetrical arrangement of the organs of Hesse with pigment cells facing the central canal.

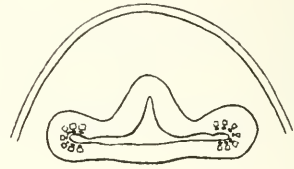


FIG. 256.—Evagination of the canal carrying with it the organs of Hesse.

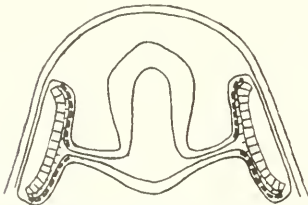


FIG. 257.—Invagination to form a sensory and pigmented layer.

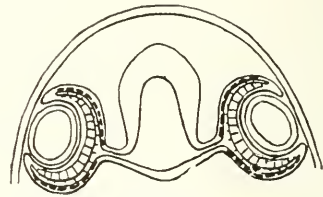


FIG. 258.—Secondary invagination of the lens vesicle (from Walls, after Boveri).

Such a development would not be unique since modified flagellated cells of this type are also seen in other sensory organs such as the olfactory cells, the hair cells of the labyrinth, the cells of the taste-buds and lateral line organs; and it is to be remembered that there is a considerable amount of evidence that the ependymal cells in the diencephalic region retain some photosensory properties in several species of Vertebrates<sup>2</sup> (von Frisch, 1911; Scharrer, 1928; Nowikoff, 1934; Young, 1935; Benoit, 1937; and others).

Agreement on the ependymal origin of the visual receptors is, however, by no means universal and many investigators, following Schwalbe, believe that they are endoneural. Thus Boveri (1904) traced their origin from the ganglion-like cells of Hesse in an *Amphioxus*-like ancestor.<sup>3</sup> In this view he was supported by Parker (1908-9),

<sup>1</sup> p. 229.

<sup>2</sup> p. 537.

<sup>3</sup> p. 230.

Tretjakoff (1913), Hescheler and Boveri (1923) and Nowikoff (1932). It was assumed that these cells became orientated in a regular manner with their associated pigment cells towards the central canal, and then were carried towards the skin in company with paired lateral diverticuli of the neural tube (Figs. 255 to 258). It is to be noted that by this hypothesis the inversion of the retina and the position of the pigmentary epithelium are also well explained. Although objections have been raised to this conception, such as the lack of ontogenetic and phylogenetic confirmation of any intermediate stages of the migration, the

FIGS. 259 TO 262.—FRORIEP'S DERIVATION OF THE ASCIDIAN (AND VERTEBRATE) EYE.

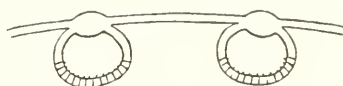


FIG. 259.

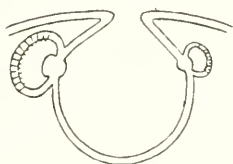


FIG. 260.

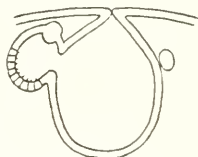


FIG. 261.

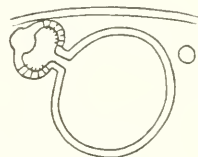


FIG. 262.

FIG. 259.—The hypothetical original existence of two sensory vesicles with an external lens and verted retina.

FIG. 260.—Involution of the neural tube showing a lens facing the neural canal and a verted retina.

FIGS. 261 and 262.—Degeneration of one eye of the original pair and migration of the lens to an external position. For simplicity the statocyst portion of the sensory vesicle is omitted.

absence of Hesse's cells in the head-end of *Amphioxus* and the danger of phylogenetic deduction from a species which appears to be an off-shoot rather than a primitive type, the theory is undoubtedly ingenious.

On the other hand, a phylogenetic analogy with the vesicular eye of the ascidian tadpole<sup>1</sup> was suggested by Lankester (1880) and strongly advocated by Jelgersma (1906). Such an ASCIDIAN HYPOTHESIS had to meet the criticism that this eye is unpaired while the presence of a lens situated on the cerebral aspect of the retina is obviously an anomaly (Fig. 235). Froriep (1906), however, suggested that the first difficulty could be overcome if the apparently unpaired eye in reality represented one of a pair; in support of his hypothesis he showed that it was situated asymmetrically towards the right and was balanced by a degenerate mass on the left which he interpreted as a

<sup>1</sup> p. 228.

vestigial eye. He attempted to overcome the second difficulty by postulating a migration of the lens from the cerebral to the superficial aspect of the vesicle; his conception of the evolution of the organ is seen in Figs. 259 to 262. If the vertebrate eye stems from an ascidian-like ancestor in this way, the formation of the tubular neural structure precedes sensory differentiation, and any superficial sensory organ associated with the surface ectoderm must be assumed to disappear and be replaced by the establishment of a neural photosensory organ. Why the dorsal and lateral areas of the neural tube should show this photosensitive differentiation raises a difficult problem; as occurs in many Invertebrates, the tendency may be associated with orientation to light coming from above, the paired lateral areas being evolved primarily in relation to orientation in the horizontal plane. The analogy, however, is by no means proved or even clear, and the danger of phylogenetic deductions in such a case is obvious<sup>1</sup>; in Froriep's (1906) view a common ancestry is more probable than a sequential derivation.

A further hypothesis, the PLACODE THEORY, usually credited to von Kupffer (1894), was suggested by Nuel (1887) and supported by Béranek (1890), Burckhardt (1902) and Lubosch (1909). It postulated the development of ectodermal placodes homologous with the lateral line organs from the anterior members of which the olfactory organs, the membranous labyrinth of the ear and the lens of the lateral eyes were developed. The lens was originally vesicular and was considered to form an eye with a verted retina; the definitive retina emerged from the central nervous system to act as its optic ganglion, homologous with a spinal ganglion, and eventually as phylogenetic evolution proceeded, took over the sensory function of the lens which degenerated into a dioptric accessory. This theory, however, has long been in disrepute since no evidence, ontogenetic or phylogenetic, connects a non-sensory retina with a sensory lens.

The origin of the lens—the other major factor in the development of the vertebrate eye—has also given rise to speculation. The homologous position of the olfactory and otic anlagen suggested first to Sharp (1885) that this structure arose from an ectodermal placode and was in its own right a sensory structure. Without attributing photosensitive properties to its cells as called for in the preceding theory of retinal development, several investigators have been attracted to the view that the lens is an independent organ derived from an anterior placode of the epibranchial series (Jelgersma, 1906; Studnicka, 1918; Schimkewitsch, 1921). The evidence of experimental embryology is conflicting. Many experimenters have established that the presence of the optic vesicle is necessary for the development of the lens, and some have claimed that this structure alone is sufficient for its determination so that a lens will form from undifferentiated ectoderm at an abnormal site if the optic cup is transplanted thereto. Others have

<sup>1</sup> See also the writings of Balfour (1878–81), Metcalf (1906), Keibel (1906), Buxton (1912), Burckhardt (1921), and others.

found that a lens may partially or completely develop if the retinal anlage has been removed from the optic plate at an early stage or in anencephalic monsters.<sup>1</sup> It may well be that there is some tendency for the formation of a lens inherent in the ectoderm of the region where it is normally found ; but on the whole, in the present stage of our knowledge, the evidence would seem to suggest that this structure is secondarily formed, called into existence normally by two mutually reinforcing inductors—the cells of the optic vesicle and the mesoderm of the head—although in certain experimental conditions no further stimulus beyond that provided by the latter may be necessary (Twitty, 1930-55 ; Woerdeman, 1950 ; Liedke, 1951).

It would seem, therefore, that despite the considerable amount of thought expended on the question, the emergence of the vertebrate eye with its inverted retina of neural origin and its elaborate dioptric mechanism derived from the surface ectoderm, is a problem as yet unsolved. Indeed, appearing as it does fully formed in the most primitive species extant today, and in the absence of transition forms with which it can be associated unless by speculative hypotheses with little factual foundation, there seems little likelihood of finding a satisfying and pragmatic solution to the puzzle presented by its evolutionary development.

- Balfour. *J. Anat. Physiol.*, **9**, 128, 408 (1878).  
*A Treatise on Comparative Embryology*, London (1881).  
 Beckwith. *J. exp. Zool.*, **49**, 217 (1927).  
 Benoît. *Bull. Biol. France Belgique*, **71**, 393 (1937).  
 Béraneck. *Arch. Sci. phys. nat.*, Genève, **24**, 361 (1890).  
 Boveri. *Zool. Jb.*, Suppl. 7, 409 (1904).  
 Bütschli. *Vorlesungen ü. vergl. Anat.*, Berlin (1921).  
 Burekhardt. *Verh. int. Zoologencong.* (1901), 621 (1902).  
 Buxton. *Arch. vergl. Ophthal.*, **2**, 405 (1912).  
 Choi. *Folia anat. japon.*, **10**, 29 (1932).  
 Dohrn. *Mitt. zool. Stat. Neapel*, **6**, 432 (1885).  
 Estable. *An. Inst. Neurol.*, Montevideo, **1**, 328 (1927).  
 Franz. *Bolk's Hb. d. vergl. Anat. d. Wirbeltiere*, Berlin, **2** (ii), 989 (1934).  
 von Frisch. *Pflügers Arch. ges. Physiol.*, **138**, 319 (1911).  
 Froriep. *Hertwig's Handbuch d. vergl. und exper. Entwicklungslehre d. Wirbeltiere*, Jena, **2** (1906).  
*Anat. Anz.*, **29**, 145 (1906).  
 Hagedoorn. *Arch. Ophthal.* (Chicago), **16**, 783 (1936).  
 Hescheler and Boveri. *Vjschr. naturf. Ges. Zürich*, **68**, 398 (1923).  
 Jelgersma. *Morphol. Jb.*, **35**, 377 (1906).  
 Keibel. *Klin. Mbl. Augenheilk.*, **44** (2), 112 (1906).  
 von Kennel. *Diss.*, Dorpat (1881).  
 Krause, W. *Arch. mikr. Anat.*, **11**, 216 (1875) ; **12**, 742 (1876).  
 von Kupffer. *Studien zur vergl. Entwicklungsgeschichte d. Kopfes d. Kranioten: II. Die Entwicklung d. Kopfes v. Ammocoetes planeri*, Munich (1894).  
 Lange. *Zbl. prakt. Augenheilk.*, **32**, 131 (1908).  
 Lankester. *Darwinism and Parthenogenesis*, London (1880).  
*Quart. J. micr. Sci.*, **31**, 445 (1890).  
 Leboucq. *Arch. Anat. micr.*, **10**, 555 (1909).  
 Leplat. *C. R. Ass. Anat.*, **17**, 194 (1922).  
 Lewis. *Amer. J. Anat.*, **3**, 505 (1904).  
 Liedke. *J. exp. Zool.*, **117**, 573 (1951).  
 Lubosch. *Morphol. Jb.*, **39**, 146 (1909).  
 Mangold. *Ergeb. Biol.*, **7**, 193 (1931).  
 Metcalf. *Anat. Anz.*, **29**, 526 (1906).  
 Müller, W. *Beit. zur Anat. und Physiol.* (Festgabe C. Ludwig), Leipzig, **2** (1875).  
 Nowikoff. *Acad. Tchèque d. Sci., Bull. internat. Clin. d. Sci. math., nat. méd.*, **33**, 131 (1932).

<sup>1</sup> See Lewis (1904), Keibel, (1906), Stockard (1910), Spemann (1912), Leplat (1923), Beckwith (1927), Mangold (1931), Choi (1932), Waddington and Cohen (1936).



- Nowikoff. *Biol. Zbl.*, **52**, 548 (1932).  
*Z. Morphol. Oekol. Tiere*, **29**, 374 (1934).  
 Nuel. *Arch. Biol., Gaud.*, **7**, 389 (1887).  
 Parker. *Amer. Nat.*, **42**, 601 (1908).  
*Amer. J. Physiol.*, **25**, 77 (1909).  
 Scharer. *Z. vergl. Physiol.*, **7**, 1 (1928).  
 Schimkewitsch. *Lehrbuch d. vergl. Anat. d. Wirbeltiere*, Stuttgart (1921).  
 Schwalbe. *Graefe-Saemisch Handbuch d. ges. Augenhk.*, Leipzig, **1**, 398 (1874).  
 Sharp. *Proc. Acad. Nat. Sci. (Phila.)*, 300 (1885).  
 Sleggs. *Amer. Nat.*, **60**, 560 (1926).  
 Spemann. *Zool. Jb., Abt. Zool. Physiol.*, **32**, 1 (1912).  
 Stockard. *Amer. J. Anat.*, **10**, 369, 393 (1910).  
 Studnicka. *Anat. Anz.*, **41**, 561 (1912); **44**, 273 (1913).  
*Zool. Jb., Abt. Anat.*, **40**, 1 (1918).  
 Tretjakoff. *Z. wiss. Zool.*, **105**, 537 (1913).  
 Twitty. *J. exp. Zool.*, **55**, 43 (1930).  
*In Analysis of Development*. Phila., p. 404 (1955).  
 Waddington and Cohen. *J. exp. Biol.*, **13**, 219 (1936).  
 Walls. *Arch. Ophthalm. (Chicago)*, **22**, 452 (1939).  
 Willmer. *Symposia Soc. exp. Biol.*, **7**, 377 (1953).  
 Woerdeman. *Ann. Biol.*, **26**, 699 (1950).  
 Young. *J. exp. Biol.*, **12**, 254 (1935).

#### THE GENERAL STRUCTURE OF THE VERTEBRATE EYE

We have seen that the eyes of Vertebrates are very true to type and (apart from a few degenerate forms<sup>1</sup>) consist essentially of a retina derived from neural ectoderm, a lens derived from the surface ectoderm, a uvea with a nutritive function, a protective tunic the anterior segment of which is transparent, and a dark chamber filled with the vitreous body, the entire organ being encased in the orbital cavity and moved by a group of extra-ocular muscles. All the variations in structure—and they are marked and of great interest—seen in the major classes within the phylum are incidental in nature and have evolved essentially as adaptations to differences in habitat or function.

Of all the ocular tissues the retina is, of course, the most important and undoubtedly the most interesting. Apart from the abundance and motility of its pigment, its occasional assumption of a tapetal function and the rare presence of oil-droplets, the pigmented epithelium shows little fundamental variation. The retina proper (the pars optica retinae) regularly comprises three layers of cells arranged in the following strata (Fig. 263) :

NEURONE I (percipient elements)	{ 1. Layer of rods and cones. 2. Outer nuclear layer. 3. Outer plexiform layer. 4. Inner nuclear layer (bipolar, horizontal and amacrine cells). 5. Inner plexiform layer. 6. Ganglion cell layer. 7. Nerve fibre layer.
NEURONE II (conductive and associative elements)	
NEURONE III (conductive elements)	

The sustentacular functions of the glial cells of the central nervous system are taken over by large fibres of Müller, the nuclei of which lie in the inner nuclear layer, while their extremities combine to form an

<sup>1</sup> p. 721.

external limiting membrane between the rods and cones and their nuclei and an internal limiting membrane on the inner surface of the nerve-fibre layer. Throughout the vertebrate phylum the structure of the retina is remarkably constant, the layers varying only in the

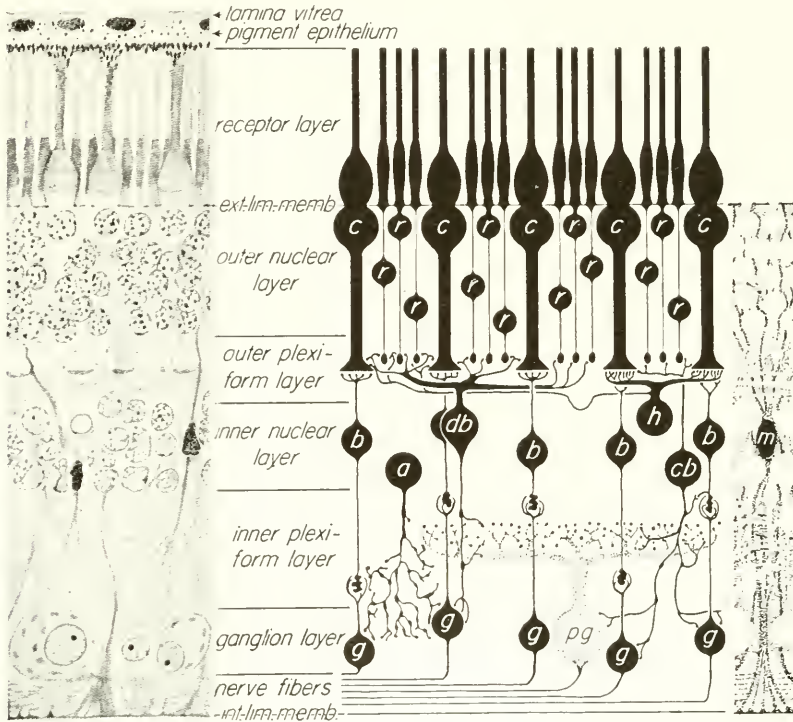


FIG. 263.—THE HUMAN RETINA.

At the left, the retina in the nasal fundus as it appears after fixation in Kolmer's fluid, nitro-cellulose embedding, Mallory's triple stain or Heidenhain's hæmatoxylin and phloxine. At the right, the neuronie hook-up of the retina, with examples of its principal elements, as revealed by the Golgi methods ( $\times 500$ ) (Gordon Walls, based largely on the work of Polyak, 1941).

*a*, amacrine cell (diffuse type); *b*, bipolar cells of ordinary "midget" type; *c*, cones; *cb*, "centrifugal" bipolar (believed to conduct outward through the retina rather than inward); *db*, diffuse bipolar cells, connecting with many visual cells, chiefly rods; *g*, ganglion cells of ordinary "midget" type; *h*, horizontal cell with dendrites connecting only with cones, axon with both rods and cones at some distance; *m*, Müller's fibre (forms limiting membranes); *pg*, "parasol" ganglion cell (one of several giant types, connecting with many bipolars); *r*, rods.

regularity of their architecture and in the density and relative preponderance of their cellular elements; even in Cyclostomes the typical layering can be recognized although the various elements tend to be intermingled, particularly the ganglion cells with the inner nuclear layer. These minor variations which occur will be noted in the subsequent chapters.

THE VISUAL CELLS constitute the most important and interesting of the constituent elements of the retina.<sup>1</sup> They have been divided into two types—rods and cones (Figs. 264–267). Typically the ROD consists of an outer and inner segment, a nucleus and a foot-piece. The outer segment, possibly representing the cilium of the ancestral

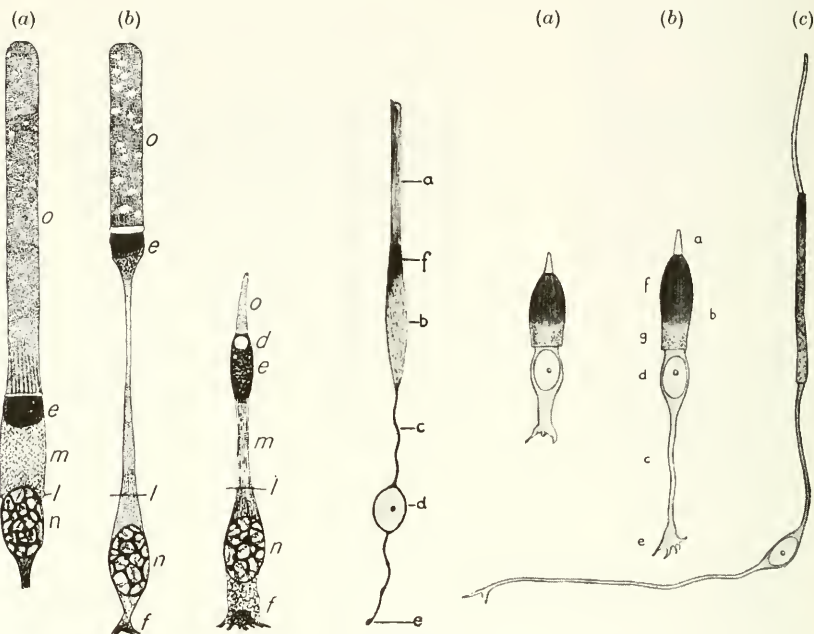


FIG. 264.

FIG. 265.

FIG. 266.

FIG. 267.

FIGS. 264 AND 265.—TYPICAL RODS AND CONES OF THE FROG, *RANA PIPIENS* (Gordon Walls).

FIG. 264.—(a) A common rod (dark-adapted); (b) a green rod.

FIG. 265.—A typical cone (dark-adapted).

d, oil-droplet; e, ellipsoid; f, foot-piece; l, external limiting membrane; m, myoid; n, nucleus; o, outer segment.

FIGS. 266 AND 267.—TYPICAL RODS AND CONES OF MAN (after Greeff).

FIG. 266.—A typical rod.

FIG. 267.—(a) A peripheral cone near the ora; (b) a peripheral cone near the equator; (c) a macular cone.

a, outer segment; b, inner segment; c, cell fibre; d, cell nucleus; e, cell foot; f, ellipsoid; g, myoid.

ependymal cell, is the photosensitive tip of the cell; the inner segment, possibly representing the columnar body of the ependymal cell, has at its outer end an ellipsoid containing mitochondria, presumably the principal site of metabolic activity, while its inner end is termed the myoid although it is by no means always contractile. The CONE has

<sup>1</sup> For structure of rods and cones, see C. Müller (1926), Wislocki and Sidman (1954), Sidman and Wislocki (1954) (histochemistry); Sjöstrand (1949–53), de Robertis (1956) (electron-microscopy); Saxén (1955–6) (development); Sidman (1957) (phase-contrast and refractometry).

the same component parts, the outer segment being typically (but not invariably) conical, the inner segment typically fatter, shorter and more squat than the corresponding part of the rod, often with an oil-droplet in the ellipsoid, and sometimes with a paraboloid composed of glycogen lying more proximally; the nucleus is relatively larger and the foot-piece more widely spread. Variations to this standard structure are common, such as the presence or absence of oil-droplets, the occurrence of double, triple or even quadruple elements, and so on; these will be discussed in the sections on systematic anatomy.

While these are the typical structural features, however, the variations in the morphology of the rods and cones are so marked as to have led to much confusion and some controversy; some rods resemble cones more closely than some members of their own family, while the cones of a well-developed fovea often resemble elongated rods more closely than typical cones (Fig. 267*c*). Indeed, in our systematic survey we shall on more than one occasion run up against difficulties in describing particular visual cells either as a rod or a cone.

Schultze (1866), who first clearly differentiated the two types of cell, did so primarily on anatomical grounds, his three criteria being—(a) the cylindrical termination of the rods in contrast to the conical tip of the cones, (b) the more external position of the cone-nuclei close to the limiting membrane owing to the shortness of the inner segment, and (c) the knob-like ending of the rods in contrast to the spread-out foot-piece of the cones. Unfortunately, all these conditions are violated, sometimes even in the same retina. The tip of the cone may be slender, elongated and cylindrical (as in lizards and birds, Verrier, 1935; Detwiler, 1943); the nuclei may lie in a single layer (amphibians, Saxén, 1953), or the usual arrangement may be reversed (some fishes and amphibians: Cajal, 1893; Franz, 1913; Menner, 1929); while the foot-pieces of rods may be branched (some fishes, amphibians and birds: Greff, 1900; Pütter, 1912; Detwiler, 1943).

Differential methods of staining have been attempted as a criterion (Dogiel, 1888; Kolmer, 1936; Wolff, 1949; Wislocki and Sidman, 1952; Saxén, 1953; and others) and again have led to inconclusive results. A further point of differentiation is a study of the connections of the visual cells; several rods are typically associated with one bipolar cell, while each foveal cone is ordinarily connected with one bipolar cell; but again, this relationship is not maintained by the peripheral cones nor in retinæ without a fovea. It is possible that, when more fully developed, the study of the ultra-microscopic structure may provide further evidence whereon a distinction between the two types of cell may be based.

The difficulty in anatomical differentiation has naturally stimulated attempts at a functional basis for classification, for it is generally conceded that the cones mediate photopic (and colour) vision while the rods are concerned with scotopic vision. The physiological distinction between "photocytes" and "scotocytes," however, is equally fraught with difficulties. The presence of rhodopsin or its relatives would theoretically substantiate the presence of rods, but while this is



possible in a uniform retina by extraction of the photopigments, the method is inapplicable in a duplex retina since the concentration of pigment is not sufficiently great to allow the histological demonstration of vitamin A even by methods so delicate as fluorescence-microscopy (Stern, 1905 ; Hopkins, 1927 ; Walls, 1935 ; Stenius, 1940 ; Greenberg and Popper, 1941 ; see Saxén, 1954 ; and others).

There is no doubt, of course, that fundamentally the two elements are alike and it is obvious that within the vertebrate phylum many transitional forms between the two exist ; between these, wherein the anatomical difficulties of differentiation occur, a sharp distinction may be illegitimate. Both are probably derived from the same primitive ancestral cells, and it has been suggested that cones are transformed into rods during development (Steinlin, 1868 ; Bernard, 1900-3 ; Cameron, 1911), a theory, however, which later evidence has questioned (Detwiler, 1943 ; Birukow, 1949 ; Saxén, 1954) ; similar criticism has been directed to the theory of Walls (1934) that the one may be transmuted into the other in phylogeny.

Walls's theory—ingenious, attractive, fanciful and much criticized—is that the primitive visual cell of Vertebrates was a cone and that therefrom rods were evolved as a transmutation-form with a view to increasing sensitivity with the development of rhodopsin—presumably first in deep-sea types. The brilliance of illumination on land allowed many reptiles (diurnal lizards) to retain a pure-cone retina ; their adoption of nocturnality as a protective measure forced some species (*Xantusia*) to develop a transitional rod-like element, and the adoption of complete nocturnality by most geckos led to the transmutation into rods. The visual elements of many snakes are similarly interpreted, the cones of some secretive nocturnal types showing a structural or a complete transmutation into rods, in the first case without, in the second with rhodopsin.

It is interesting that recent research has to a considerable extent confirmed this somewhat revolutionary view. That such a transmutation had in fact occurred is suggested by the finding of Crozier and Wolf (1939) that the rod-retina of the gecko, *Sphaerodactylus*, has a critical fusion frequency similar to that obtained in the turtle with its predominantly pure-cone retina. The same conclusions could be said to follow the finding of Underwood (1951) that some primitive Jamaican geckos had oil-droplets in their rod-like receptors. The peculiar pigment with its unusual absorption curve for a substance based on vitamin A<sub>1</sub> (maximum at 524 mμ) described in certain geckos by Denton (1953) (*Gekko gekko*) and Crescitelli (1956) (*Phyllurus*) again could perhaps be interpreted as an attempt to transform ancestral cones into rods, as if they were unable to re-invent rhodopsin for lack of the suitable protein, and had thus been forced to conjugate their retene<sub>1</sub> as a chromophore and produce a pigment with an absorption intermediate in spectral position between those generally

accepted as typical of rod-pigments and cone-pigments. Finally, the observations of Bellairs and Underwood (1951) support the view that snakes were derived from burrowing lizard-like ancestors.

In the present state of our knowledge the problem, which raises questions as difficult as they are interesting, is unsolved.

Combinations of these visual elements are frequently encountered in several classes of the vertebrate phylum. Double rods are rare (geckos and some nocturnal snakes). A second rarity is the twin cones—a fusion of identical elements—which are found only in Teleosteans (Figs. 347–8). Double cones are more common, appearing first in Holosteans and occurring in every other class.<sup>1</sup> Typically they represent the fusion of two unlike elements, the principal resembling the single cones in the same retina and the accessory, generally of a simpler type, rarely containing an oil-droplet but frequently an unusually large paraboloid. In Amphibians, Saxén (1954–56) has brought forward evidence that the double visual elements represent not the fusion of two cones as has generally been thought but the fusion of a rod with a cone. Triple “cones” (perhaps two cone-like components with a third rod-like component, Saxén, 1953) occur in some Teleosts (trout) and Anurans, while quadruple elements have also been described in the minnow, *Phoxinus* (Lyall, 1956).<sup>2</sup>

The origin of these double cells has given rise to some controversy. The sceptical view that they were histological artefacts was put forward by Koganei (1884) and has been maintained by such writers as Cameron (1911) and Roze-meyer and Stolte (1930). There seems no doubt, however, that they do exist. Dobrowolsky (1871) put forward the hypothesis that they resulted from the incomplete division of single cones, a view upheld by Howard (1908) and Franz (1913). On the other hand, Detwiler and Laurens (1921), finding that double cones appeared during development at a stage when no further cell-divisions took place, suggested that they were produced by the fusion of two separate progenitors; this view has been well substantiated in Amphibians by Saxén (1954–56).

The physiological significance of the association of more than one visual cell is not understood. The fact that the dendrites of the two components sink to different depths in the outer plexiform layer suggests some difference in function (Cajal, 1893; Greeff, 1898), while the observation of v. Genderen-Stort (1887) that photomechanical reactions are confined to the principal elements points to the probability that the accessory element has a subsidiary function. Whether this is visual or metabolic, the two elements living in symbiosis (Howard, 1908; Franz, 1913), is conjectural.

Apart from the fundamental structure of the retina the other ocular tissues, although in general conforming to the vertebrate plan seen in man (Fig. 268), show considerable variations depending upon

<sup>1</sup> Many Teleosts, *Protopterus*, Amphibians, Reptiles except some snakes, Birds, the platypus, and Marsupials.

<sup>2</sup> See also footnote, p. 364.

an unusually wide range of adaptive demands, for vertebrates have succeeded in making themselves at home in every environment where life is possible. These differences have been very considerable and the adaptations demanded have been great. The vertebrate eye was initially evolved for vision in shallow water; it has been asked to adapt itself for vision in the abyss, in the rivers, in the mud of the swamps, on land and in the air, and on occasion to readapt itself for

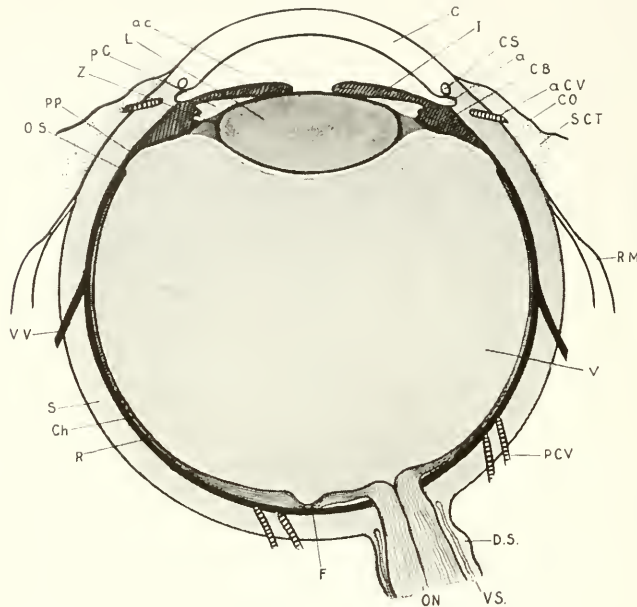


FIG. 268.—DIAGRAM OF THE LONGITUDINAL SECTION OF THE HUMAN EYEBALL.

a, angle of anterior chamber. ac, anterior chamber. aCV, anterior ciliary vessel. C, cornea. CB, ciliary body. Ch, choroid. CO, ocular conjunctiva. CS, canal of Schlemm. DS, dural sheath. F, fovea. I, iris. L, lens. ON, optic nerve. OS, ora serrata.

PC, posterior chamber. PCV, posterior ciliary vessel. PP, pars plana. R, retina. RM, rectus muscle. S, sclera. SCT, subconjunctival tissue. V, vitreous. VS, vaginal sheath. VV, vortex vein. Z, zonule.

vision in the seas; it has been asked to fit itself for vision at night, in twilight or in dark cavernicolous surroundings and in the brightest of daylight; it has been asked to cater for panoramic vision where the detection of movement is paramount, or to accommodate itself to the finest stereoscopic prowess, to meet the needs of a sluggish or an active habit of life, to be content with a vague apperception or to evolve the capacity for minute resolution in form vision and master the intricacies of colour vision. All this—and more—it has done; and in so doing it has tried and often discarded, now this expedient, now that.

The requirements of aerial vision when Amphibians left the water for the dry land were met by an optical reorientation of the primitive aquatic eye to suit the new medium and the provision of lids equipped with elaborate glandular structures as a protection against drying ; a return to water (as in the whale or the dolphin) has led to a reversion of this process. The requirements of an amphibious life have resulted in the adoption of a host of ingenious devices to allow an easy transition from one medium to the other and to maintain adequate vision in each. The dangers of a burrowing habit or a sandy environment have led to the acquirement of protective "spectacles" (in lizards and snakes). The vagaries of nocturnal, crepuscular or diurnal vision are met by several expedients—variations in the size of the eye and the lens, in the relative proportions of the percipient elements in the duplex retina, in the size, shape and motility of the pupil, and the provision of a tapetum or argentea, choroidal or retinal in site, fibrous, cellular or crystalline in nature, which augments a scanty supply of light by its mirror-like effect. The requirements of acuity of vision are met by the development of an area centralis and a fovea, the receptor elements of which are provided with individual nervous connections ; stereopsis by the provision of more than one fovea or by a swinging forward of the visual axes ; focusing at varying distances by a host of accommodative devices—the development of accessory retinae close to the dioptric apparatus (as in the tubular eyes of deep-sea fishes), variations in the position of the visual cells relative to the lens (as in some bats or in the horse), the use of a stenopæic pupil (as in the gecko or the cat), the deformation of the eye by muscular action from outside (as in the lamprey), the pushing or pulling of the lens backwards or forwards (as in some Fishes, Amphibians and snakes), or a change in its shape by squeezing it (as in Reptiles and Birds) or relaxing it (as in Mammals). These serve to illustrate the multitude of expedients adopted by an organ of unique plasticity to meet the requirements of environments so completely different as the abyss of the ocean and the upper air, or habits so diverse as the sluggishness of a parasite and the activity of a bird-of-prey.

The general scheme of phylogenetic development of the vertebrate eye is therefore interesting in that it does not show a steady and gradual increase in efficiency, but illustrates the elaboration of more than one type from a common beginning along different lines to reach more than one culminating point. The common beginning may be found in Cyclostomes, the eyes of which are primitive and show no specializations. From this starting point three peak-points have evolved in types which in their habits of life are peculiarly visually conscious—in teleostean Fishes, Sauropsida (lizards and Birds) reaching its highest development in Avians, and among Mammals in



the Primates. In these three groups alone is a fovea found making possible a good acuity of vision ; in these, highly developed accommodative mechanisms are present allowing accuracy of form vision over a wide range of distances ; and in these alone good colour vision has been demonstrated. In each of these the optic axes may be swung forwards so that the visual fields are made to overlap, thus rendering it possible for binocular to replace panoramic vision ; in the last group a partial decussation of the optic nerve fibres allows an anatomical basis for the coordination of ocular movements ; and finally, a neopallium built up upon the sense of vision replaces the original archipallium which was based upon the sense of smell. In this way the dyscritic mechanism of the simple eye of the lower Vertebrates, which was essentially adapted to the biologically primitive function of the appreciation of light and movement, developed the capacity for the intelligent appreciation of complex visual patterns and the potentiality to form reasoned visual judgements.

The interesting thing is that the eye of each of these types has developed separately and independently ; between them there is no evolutionary sequence, for all have attained their high degree of efficiency by different expedients which, when they show affinities, owe their relationship to the fact that they have evolved not the one from the other, but all from the same original substrate of physiological potentialities. It is also interesting that of these types the sauropsidan eye is the most efficient as an optical mechanism ; of all the three, Birds have relatively the largest and absolutely the most specialized eyes, the most efficient focusing apparatus, a pecten structure instead of a retinal system of vessels, the most complex macular arrangements, and the highest visual acuity. The eye of man cannot therefore be considered as representing the acme of efficiency as an optical instrument ; it is to the unique and transcendent development of the associated cerebral centres that it owes its functional predominance.

- Bellairs and Underwood. *Biol. Rev.*, **26**, 193 (1951).  
 Bernard. *Quart. J. micr. Sci.*, **43**, 23 (1900) ; **44**, 443 (1901) ; **46**, 25 (1903).  
 Birukow. *Z. vergl. Physiol.*, **31**, 322 (1949).  
 Cajal. *La Cellule*, **9**, 119 (1893).  
 Cameron. *J. Anat. Physiol.*, **46**, 45 (1911).  
 Crescitelli. *J. gen. Physiol.*, **40**, 217 (1956).  
 Crozier and Wolf. *J. gen. Physiol.*, **22**, 555 (1939).  
 Denton. *XIX Internat. Cong. Physiol., Abstr. Communications*, 306 (1953).  
 Detwiler. *Vertebrate Photoreceptors*, N.Y. (1943).  
 Detwiler and Laurens. *J. comp. Neurol.*, **33**, 49 (1921).  
 Dobrowolsky. *Arch. Anat. Physiol.*, 208 (1871).  
 Dogiel. *Anat. Anz.*, **3**, 133 (1888).  
 Franz. *Oppel's Lhb. vergl. mikr. Anat. Wirbeltiere*, Jena, **7**, 1 (1913).  
 van Genderen-Stort. *v. Graefes Arch. Ophthal.*, **33** (3), 229 (1887).  
 Greeff. *Z. Psychol. Physiol.*, **16**, 161 (1898).  
 Graefe-Saemisch *Hb. ges. Augenheilk.*, **II**, **1**, Kap. 5 (1900).  
 Greenberg and Popper. *Amer. J. Physiol.*, **134**, 114 (1941).  
 Hopkins. *Z. vergl. Physiol.*, **6**, 345 (1927).  
 Howard. *J. Morphol.*, **19**, 561 (1908).  
 Koganei. *Arch. mikr. Anat.*, **23**, 335 (1884).

- Kolmer. Möllendorff's *Hb. mikr. Anat. d. Menschen*, **3** (2), 310 (1936).
- Lyall. *Nature (Lond.)*, **177**, 1086 (1956).
- Menner. *Z. vergl. Physiol.*, **8**, 761 (1929).
- Müller, C. *Z. Anat. Entwickl. Ges.*, **81**, 220 (1926).
- Pütter. *Graefe-Saemisch Hb. ges. Augenheilk.*, **III**, **1**, Kap. 10, 1 (1912).
- de Robertis. *J. biophys. biochem. Cytol.*, **2**, 319; suppl., 209 (1956).
- Rozemeyer and Stolte. *Z. mikr. Anat. Forsch.*, **23**, 98 (1930).
- Saxén. *Ann. Mcd. exp. Biol. Fenn.*, **31**, 254 (1953).
- Ann. Acad. Sci. fen. A IV*, **23**, 1 (1954).
- Acta Anat.*, Basel, **25**, 319 (1955).
- J. Embryol. exp. Morphol.*, **4**, 57 (1956).
- Schultze. *Arch. mikr. Anat.*, **2**, 175 (1866); **3**, 215 (1867).
- Sidman. *J. biophys. biochem. Cytol.*, **3**, 15 (1957).
- Sidman and Wislocki. *J. histo-chem. Cytochem.*, **2**, 413 (1954).
- Sjöstrand. *J. cell. comp. Physiol.*, **33**, 383 (1949); **42**, 15, 45 (1953).
- Steinlin. *Arch. mikr. Anat.*, **4**, 10 (1868).
- Stenius. *Acta Physiol. Scand.*, **1**, 380 (1940).
- Stern. *v. Graefes Arch. Ophthalm.*, **61**, 561 (1905).
- Underwood. *Nature (Lond.)*, **167**, 183 (1951).
- Verrier. *Bull. Biol. France Belg.*, Suppl. **20**, 1 (1935).
- Walls. *Amer. J. Ophthalm.*, **17**, 892 (1934).
- Brit. J. Ophthalm.*, **19**, 129 (1935).
- The Vertebrate Eye*, Michigan (1942).
- Wislocki and Sidman. *Anat. Rec.*, **113**, 540 (1952).
- J. comp. Neurol.*, **101**, 53 (1954).
- Wolff. *The Anatomy of the Eye and the Orbit*, London (1949).