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SYSTEM OF OPHTHALMOLOGY

The scheme for the "System of Ophthalmology" is as follows, but its division into different volumes is liable to alteration.

- Vol. I. THE EYE IN EVOLUTION
- Vol. II. THE ANATOMY OF THE VISUAL SYSTEM
- Vol. III. NORMAL AND ABNORMAL DEVELOPMENT
 - Pt. I. EMBRYOLOGY
 - Pt. II. CONGENITAL DEFORMITIES
- Vol. IV. THE PHYSIOLOGY OF THE EYE AND OF VISION
- Vol. V. OPHTHALMIC OPTICS AND REFRACTION
- Vol. VI. OCULAR MOTILITY AND STRABISMUS
- Vol. VII. THE FOUNDATIONS OF OPHTHALMOLOGY
 - HEREDITY, PATHOLOGY, METHODS OF DIAGNOSIS,
GENERAL THERAPEUTICS
- Vol. VIII. DISEASES OF THE OUTER EYE
 - Pt. I. CONJUNCTIVA
 - Pt. II. CORNEA AND SCLERA
- Vol. IX. DISEASES OF THE UVEAL TRACT
- Vol. X. DISEASES OF THE RETINA
- Vol. XI. DISEASES OF THE LENS AND VITREOUS;
GLAUCOMA AND HYPOTONY
- Vol. XII. NEURO-OPHTHALMOLOGY
- Vol. XIII. THE OCULAR ADNEXA
 - LIDS, LACRIMAL APPARATUS, ORBIT AND PARA-
ORBITAL STRUCTURES
- Vol. XIV. INJURIES
- Vol. XV. INDEX OF GENERAL AND SYSTEMIC
OPHTHALMOLOGY

SYSTEM OF OPHTHALMOLOGY

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VOL. I

THE EYE IN EVOLUTION

BY

SIR STEWART DUKE-ELDER

*WITH 902 ILLUSTRATIONS, 15 COLOURED PLATES
AND 350 MARGINAL ILLUSTRATIONS*



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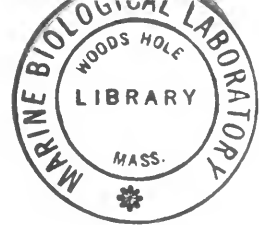
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PREFACE

THE reception accorded to my Textbook of Ophthalmology has persuaded me that there is a need for its continuation in a second edition. The seven volumes of the Textbook took almost a quarter of a century to write, a period unfortunately longer than it might have been owing to the exigencies of war. The first four volumes have long been out of print—and intentionally so because they have long been out of date. It is to be remembered that the second volume was written before the sulphonamides were introduced ; the third before the antibiotics revolutionized the therapeutics of infective diseases ; both of them before the role of viruses in ocular disease was adequately appreciated ; the physiology of the eye of yesterday is unrecognizable when compared with that of today ; even the anatomy has been transformed by more elaborate optical and chemical methods of investigation and the advent of the electron microscope. The re-writing of the whole work if its comprehensive nature were to be retained would be an immense task occupying more time than I could reasonably expect to have at my disposal. Moreover, tomorrow will be different from today, and if a work such as this is to be of any lasting value it would seem to me desirable that a new edition be published at least every fifteen or twenty years ; fortunately, ophthalmology is no static science.

It therefore seemed to me wise to share the task of re-writing the original Textbook with my colleagues at the Institute of Ophthalmology in London. I am grateful that they have accepted this burden. For this reason I have changed the name of the book to a "System of Ophthalmology" since it will necessarily be less personal.

This first volume in the new series is an extension of the first twenty pages of Volume I of the old Textbook ; this I have written myself, largely because it is a subject in which I am particularly interested—and I wished to write it. The subject-matter has never been gathered together in a single book before and it is my hope that it will interest ophthalmologists in so far as it forms the basis of the science of vision : and it may be that it will be of value also to those whose interest is biological rather than clinical.

The numerous marginal sketches are not usual in a book of this type. To the student of natural history they may seem superfluous, but to the ophthalmologist some of the animals may be unfamiliar and the drawings may perchance add meaning to the zoological nomenclature and thus give the text more life and interest. It is to be noted, however, that they are drawn not to scale, but approximately to a standard size to fit into a 1-inch margin.

STEWART DUKE-ELDER.

INSTITUTE OF OPHTHALMOLOGY,
LONDON,
1957.

ACKNOWLEDGEMENTS

IN the preparation of this book I have incurred a considerable amount of indebtedness which is a pleasure to record.

Many of the illustrations are borrowed, and in each the source is acknowledged. There are, however, five sources from which I have liberally drawn, and these merit special thanks : Dr. Gordon Walls, for a number of his original drawings ; Masson et Cie of Paris, who have allowed me to use some illustrations from Rochon-Duvigneaud's classical work, *Les Yeux et la Vision des Vertébrés* ; Dr. Maurice Burton and his publishers, the Elsevier Publishing Co. of Holland, for some illustrations from *The Story of Animal Life* ; the Royal Society for permission to use a large number of Lindsay Johnson's illustrations published in their *Proceedings* ; and Macmillan & Co. for giving free permission to copy a large number of the illustrations of animals in the *Cambridge Natural History* in the form of marginal sketches.

In preparing the illustrations I have had the willing co-operation of Dr. Peter Hansell and the Department of Medical Illustration of the Institute of Ophthalmology, the assistance of which, particularly that of Mr. T. R. Tarrant, the Medical Artist, has been invaluable. The Zoological Society of London has lent me a number of photographs, as also has the Natural History Museum of London, together with specimens of various invertebrates. Professor Ida Mann has allowed me to use a large number of her illustrations of the eyes of animals, and Dr. Kevin O'Day of Melbourne has allowed me to use photographs and slides of the eyes of Monotremes and Marsupials which are unobtainable outside Australia ; while in this Institute Professor Norman Ashton and Dr. Katharine Tansley have provided me with sections and photographs of the eyes of a number of animals.

In several instances my knowledge of zoology has been brought up to date by the great kindness of Dr. Mary Whitear of the Zoology Department of University College, London, who has read the proofs of those sections dealing with zoological classification ; while Dr. Katharine Tansley and Dr. Robert Weale of this Institute have given me most helpful criticism in some aspects of the visual problems discussed. Miss M. H. T. Yuille, Mr. A. J. B. Goldsmith and my wife have shared with me the onerous task of proof-reading.

It is difficult for me to express my indebtedness to my secretary, Miss Rosamund Soley, who has borne much of the burden of the technical aspects of the production of this Volume. She has typed and prepared the manuscript, corrected the proofs, and undertaken the immense and somewhat thankless task of verifying the bibliographies, prepared the Zoological Glossary and the Index, and drawn the 350 marginal sketches.

Finally, my indebtedness to my publishers, Henry Kimpton, continues to be immense. They have assisted me in every possible way. Why Mr. G. E. Deed continues to put up with my moods and vagaries after thirty years is to me quite incomprehensible.

STEWART DUKE-ELDER.

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PART I
THE EFFECT OF LIGHT ON LIVING ORGANISMS

INTRODUCTION

THE EFFECT OF LIGHT ON METABOLISM

THE EFFECT OF LIGHT ON MOVEMENT

THE EFFECT OF LIGHT ON PIGMENTATION

THE EMERGENCE OF VISION

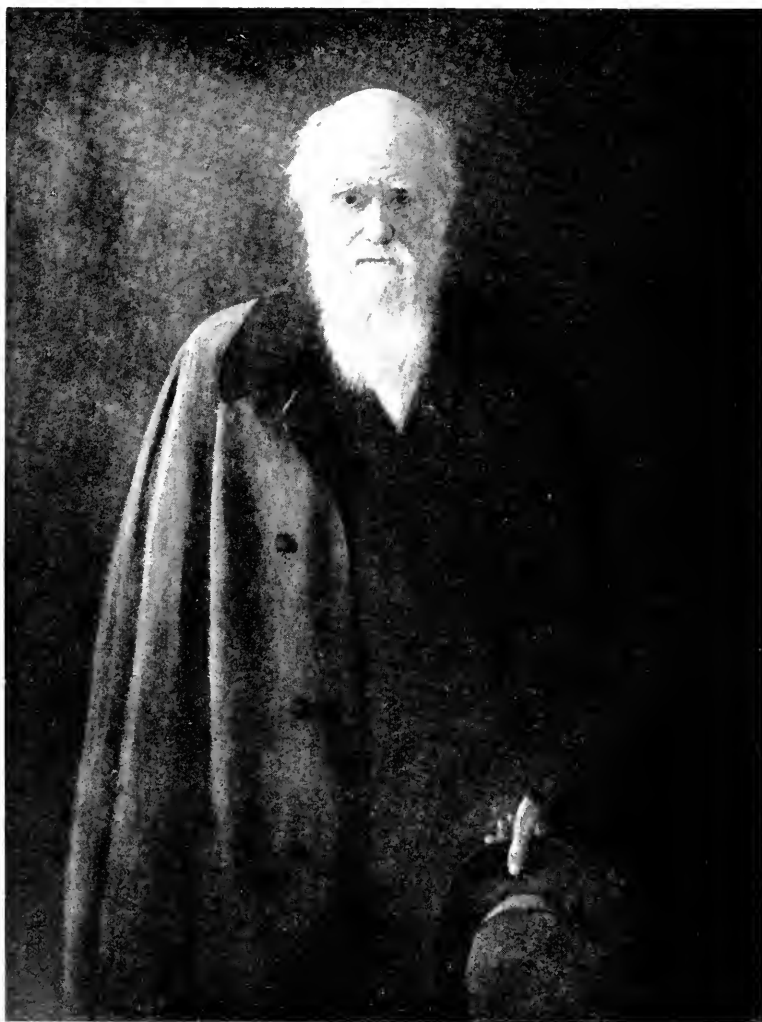


FIG. 1.—CHARLES DARWIN (1809–1882).
(From a portrait by John Collier in the Linnean Society.)

CHAPTER I

INTRODUCTION

WE begin with a drop of viscid protoplasm the reactions of which we do not understand, and we end lost in the delicacy of the structure of the eye and the intricacies of the ten thousand million cells of the human brain. We begin with photosynthesis in a unicellular plant, or with a change in the viscosity produced by light in the outer layers of the amoeba, and we end with the mystery of human perception. We begin some one or two thousand million years ago in the warm waters of the Archeozoic era and we end with the speculations of tomorrow. And as we travel together tracing the responses of living things to light from the energy liberated by a simple photochemical reaction to the faculty of appreciating and interpreting complex perceptual patterns, neither in fact nor in fiction does a story more fascinating unfold. It is a story which traces a development from a vague sentience to apperception, from vegetative existence to the acquisition of the power to mould the environment, from passive reactivity to the ability to create history. Nor is there a story more important. Even at the physiological level some 38% of our sensory input is derived from the retina,¹ impulses from which, even in the complete absence of visual stimuli, are largely responsible for maintaining a tonic influence upon the level of spontaneous activity in the brain.² From the psychological point of view the importance of vision is still greater. If, indeed, the proper study of mankind is Man, and if (as we must agree) his behaviour and his contact with the outside world are mediated through his senses, what can be more fundamental than the study of the sense which, more than any other, determines his intelligence and regulates his conduct, of the faculty which eventually played the preponderant role in assuring his dominance and determining his physical dexterity and intellectual supremacy? We are indeed highly visual creatures.

It would seem appropriate to introduce a book devoted to the evolution of vision with a portrait of CHARLES DARWIN (1809–1882) (Fig. 1), the great English naturalist who, like Newton in the world of physics, was one of the very few men who revolutionized world thought in the subject on which he worked—and beyond. But Darwin has a special claim to introduce this chapter, for at a time when the conduct of animals was generally ascribed to the existence of vital forces or psychic activities, and when the orientation of plants was thought to be due to the direct influence of physical stimuli such as light and heat upon the

¹ According to the calculations of Bruesch and Arey (*J. comp. Neurol.*, **77**, 631, 1942).

² See Claes (*Arch. intern. Physiol.*, **48**, 181, 1939) and many others, admirably summarized in Granit (*Receptors and Sensory Perception*, New Haven, 1955).

plant as a whole, he transformed biology to a more factual plane based on observation and experiment, and was the first to show that in the higher plants receptor tissues existed separately from motor tissues, and that the orientation of plants to light was due to the transference over some distance of stimuli appreciated by the former to be made effective by the latter. These observations which appeared in the last of the classical books derived from his pen¹ form a typical example of the revolutionary nature of Darwin's philosophy—the result of a unique combination of experimental genius with penetrative powers of interpretation which have rarely been equalled—and from these observations have directly followed our understanding of the development of the sensory organs and their effect on the evolution of the higher species in the animal scale.

The son of a doctor in the English country town of Shrewsbury, he went to the University of Edinburgh to study medicine ; this, however, he forsook and went to Cambridge with the intention of entering the Church ; but here Sedgwick and Henslow, the professors of geology and botany, inspired him again with a love of natural history which eventually was to become a passion. Darwin's assessment of the qualities responsible for his own success is worth remembering : "the love of science, unbounded patience in long reflecting over any subject, industry in observing and collecting facts and a fair share of invention as well as of common sense". And again : "I have steadily endeavoured to keep my mind free so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject), as soon as facts are shown to be opposed to it".²

THE RESPONSES OF ORGANISMS TO LIGHT

LIGHT—the visible radiant energy derived from the sun—is responsible for the whole existence of living things on the earth, and without question PHOTOSYNTHESIS IN PLANTS—the reaction whereby the carbon dioxide and water which permeate the atmosphere and the earth's crust are converted into the organic substances which constitute the basis of all living things—is the most fundamental and important chemical process on our planet. Not only was photosynthesis responsible for the origin of life but it maintains the perpetual cycle of the activities of living things. By oxidation, living structures are continuously broken down to their initial constituents (carbon dioxide and water), the process being accompanied by the liberation of the energy required by organisms to perform their varied activities ; by photosynthesis the carbon dioxide and water produced by the oxidation of living matter are perpetually reunited by an opposite process of reduction with the return of oxygen to the atmosphere, the high energy requirements necessary being supplied by the capacity of the chlorophyll group of pigments in green plants to absorb sunlight. This reaction whereby the chlorophyll system stores and then liberates light-energy is thus not only the source of the activities of all living things but supplies much of the energy at the disposal of the civilized world in the stores of coal and petroleum formed throughout the ages.

¹ *Power of Movements in Plants*, London, 1880.

² *Life and Letters of Darwin*, by Francis Darwin, 1887.

It would be out of place to enter fully into the mechanism of photosynthesis by chlorophyll here ; for a recent summary the reader is referred to the monograph by Hill and Whittingham.¹ The chlorophyll group of pigments are tetrapyrrolic compounds in which magnesium is present in non-ionic form ; they are related to hæmin which, however, contains a central iron atom. The completed process whereby carbohydrates are synthesized has long been known and may be represented by the equation :



The intimate mechanism, however, has only recently begun to be analysed, an advance largely due to the use of radio-active carbon (¹⁴C) as a "tracer". Although many of the details are still obscure, particularly the way in which chlorophyll absorbs radiant energy and directs it into chemical processes, the basic reactions are known and can indeed be carried out in the test-tube. The essential process is the photolysis of water. Chlorophyll induces the energy derived from light to break the hydrogen-oxygen bonds in the molecule of water ; the hydrogen therefrom is used to convert the single carbon atoms of CO₂ into long-chained carbohydrates through the medium of phosphoglyceric acid and the oxygen is liberated as a free gas ; meantime a store of chemical energy is provided by the photosynthesis of energy-rich compounds such as adenosine triphosphate, the break-down of which by simple hydrolysis releases large amounts of energy to drive the process. It is probable that these and the many other compounds found in plants are formed by enzyme-reactions from one or more of the constituents of the photosynthetic cycle at either the C₃ or C₆ level.²

Apart from this basic activity which characterizes the vegetable world, light produces photochemical reactions of great variety in living organisms. The energy thus liberated produces in the most primitive creatures the only response available—a change of general activity, frequently of motion, just as do other stimuli, mechanical, gravitational, thermal, chemical or electrical ; in the higher forms a multitude of activities may be initiated or influenced.

These responses we will review under four main headings. In the first place, the response may take the form of a *change in general metabolic activity*, usually, but not invariably, an increase of activity under the influence of light. As a natural extension of this, the diurnal cycle of light and darkness has in the course of evolution so impressed itself upon a number of the fundamental activities of many organisms (including man) that these show a corresponding rhythm which has eventually become innate and endogenous (photoperiodism). In the second place, the response may be expressed as a *variation in movement*. In its simplest form this is also merely a change in general activity wherein movements are random in nature and undirected (photokinesis) ; as an evolutionary extension of this the movements initiated by light come under the directional control of the stimulus so that the organism is orientated by light in a definite way ; such movements

¹ *Photosynthesis*, London, 1955. See also *Proc. roy. Soc. B*, **157**, 291 (1963).

² For reviews, see Arnon (*Ann. Rev. plant Physiol.*, **7**, 325, 1956, *Nature* (Lond.), **184**, 10, 1959), Rosenberg (*Ibid.*, **8**, 1957).

may affect the component parts of sessile organisms (phototropism) or may be expressed in translatory movements by motile organisms (phototaxes). In the third place, light acting directly or indirectly is the most potent stimulus for *altering the pigmentary distribution* in both plants and animals—an understandable reaction since pigment has been evolved specifically for the absorption of light, either to utilize its energy or as a protection against its excess.

All these activities have become more complex as evolution has proceeded. The most primitive required no specific organization; the more complex called for the acquisition of one or more receptor organs, which in their most elementary stages need appreciate only changes in the intensity of the light, but in their more advanced forms must analyse the direction of its incidence and its spatial distribution. Initially, in some unicellular organisms a diffuse reactivity sufficed; but as multicellular organisms developed, the stimulus must needs be transported to the effector organs, either chemically by hormones or by nervous activity. In this way the effects of light upon metabolism, orientation and pigmentation became correlated through primitive nerve-nets and then became integrated in the ganglia of the central nervous system; and eventually, when the nervous pathways from the eyes were projected into a head-ganglion and ultimately into the fore-brain, the highly complex faculties of *vision* and *apperception* evolved.

CHAPTER II

THE EFFECT OF LIGHT ON METABOLISM

It is well known and universally recognized that the general behaviour of many organisms is regulated by light ; the contrast between the activities of nature by day and its stillness by night needs no stress. This is a widespread characteristic of vegetable life which exists so much more closely to the sun and the earth than do animals, but even among the latter dramatic changes are frequently evident, particularly in the lower forms. Thus among Protozoa, some Rhizopods change their form, contracting under the influence of light (Engelmann, 1882 ; Verworn, 1889) (Figs. 2 and 3), many species are activated by light (such as flat-worms, Loeb, 1893-94), while other creatures become inactive under its influence (maggots, Herms, 1911 ; and many insects, such as cockroaches, Gunn, 1940). Among the higher forms of life, in addition to a number of basic metabolic functions, the reproductive

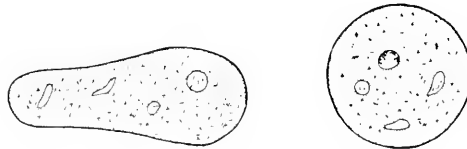


FIG. 2.

FIG. 3.

FIGS. 2 AND 3.—*Pelomyxa palustris* at rest (Fig. 2), and contracted under the influence of light (Fig. 3).

cycle and secondary features such as colour changes and behavioural habits are similarly regulated by light although in many cases other factors such as temperature, humidity and nutrition exert sometimes contributory, sometimes more potent effects. In this way the alternation of day and night has imposed a rhythmic diurnal cycle upon a number of the activities of living organisms (PHOTOPERIODISM) ; and it is to be remembered that in many of the phenomena thus involved darkness seems to be as important a stimulus as light. Indeed, in many cases the rhythm has become so fundamental that if the organism is placed in experimental circumstances wherein the natural alternation of light and darkness is changed to become out-of-phase, or if it is exposed to continuous light or darkness, many of these cyclic changes continue as if the normal 24-hour rhythm still persisted ; the rhythm originally imposed by external circumstances has eventually become autochthonous.



FIG. 4.—CARL LINNÆUS (1707–1778).

Carl Linnæus, son of a Lutheran Swedish pastor and Professor of Botany at Uppsala, is universally acknowledged as the Father of Scientific Botany. His main work was his *System of Nature* which passed through 12 editions in his lifetime following its initial publication in 1741. He had a passion for classification. Not only did he classify in a system based on their reproductive organs the 18,000 species of plants known to him, which he and his pupils travelled far and wide to collect (one of them, for example, accompanied Captain Cook on his first voyage, 1768–71); but he also classified animals, diseases and minerals—even past and present scientists in a system of military rank with himself as general. He introduced the now universally adopted nomenclature of plants and animals, first the *generic* name indicating the genus, and second the *specific* name indicating the species. His garden is still tended in Uppsala. The Linnean Society of London which possesses his library and collections was founded in 1788.

This portrait of “Carl v. Linné ætat. 67”, lent me by the Linnean Society, is from the original by Krafft, the Swedish artist, who painted it in 1774 for the College of Physicians at Stockholm of which Linnaeus was one of the founders.

The origin of such rhythms is speculative, but it is interesting to recall the environment of living creatures when first they experienced the drama of a day-night cycle on the earth. For millions of years living organisms never experienced conditions more varied than those of the warm but placid sea, but as the seaweeds of the swamps spread onto the land, plants became exposed alternately to the stimulating conditions of a humid hot-house during the day and the depression of the comparative chill of night. Similarly, as Amphibians emerged to creep upon the land in the heat of the Palaeozoic, and as they and the Reptiles matured in the torrid Jurassic and Cretaceous ages, it is difficult to realize the violence of the contrast between the extreme metabolic and nervous activity which must have occurred in the blaze of noon, and the sluggishness of sleep and the reduction of nervous energy which must have prevailed in the cold of night; for chemical activity and the speed of nervous impulses are both dependent on temperature. It is probable, indeed, that the development of thermostasis and its ultimate evolution into homeostasis were the determining events which made possible the evolution and ultimate supremacy of Birds and Mammals on a cooling globe, and that the lack of the control of temperature was the main cause of the extinction of the Dinosaurs and the retreat of the Amphibians to a few degenerate types. But it is to be remembered that the period during which the primitive creatures which first inhabited the still-warm earth experienced this alternating climax of delirious activity each noon and fatigued torpidity each night, occupied some hundred million years; and even although their descendants have long acquired the peace of the thermostasis, it is not surprising that traces of the early turmoil still remain.

PHOTOPERIODISM IN PLANTS

Over 200 years ago, CARL LINNÆUS (1707–1778) (Fig. 4), who laid the groundwork of scientific botany at Uppsala, noted that many

FIGS. 5 AND 6.—SLEEP MOVEMENTS IN FLOWERS AND LEAVES.

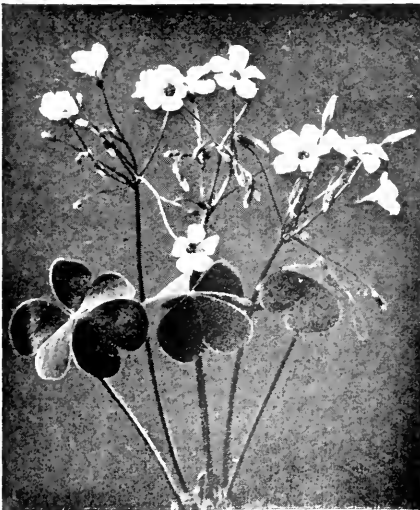


FIG. 5.—*Oxalis rosea* awake.

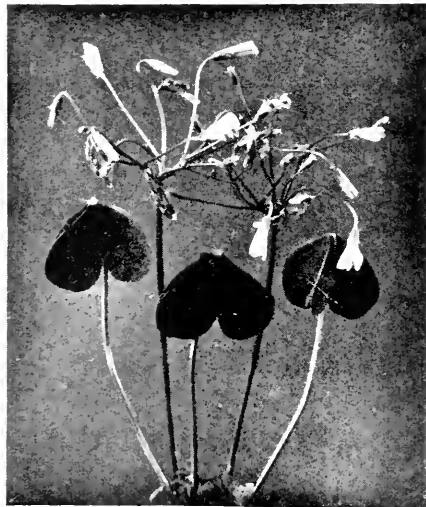


FIG. 6.—*Oxalis rosea* asleep.

flowers have a time of opening and closing so regular that he constructed a flower-clock from which the time of day could be read—the poppy opened at 6 a.m., the speedwell at mid-morning, the white campion in the evening (to be pollinated by night moths), and so on (Figs. 5 and 6). At a much later date, the “sleep movements” of leaves were similarly studied by Darwin (1880): those of the runner bean, for example, raise themselves during the morning, become horizontal by noon, fall in the afternoon and fold up at night. The significance of these daily rhythms, however, was largely neglected until they were intensively investigated by the German botanist, E. Bünning (1931–56), who showed that they were not simply an immediate response to the passing stimuli of day and night, but were part of a rhythmic change which has become characteristic and endogenous to the plant itself—a 24-hour rhythm in the intensity of endosmosis throughout its structure, in the rate of growth, the rate of respiration, the activity of enzymes and the entire metabolism, a rhythm to which the plant has become habituated so that the periodicity persists for some time even if it is placed in continuous darkness, and is only slowly readjusted if an artificial rhythm is imposed upon it.¹ Other factors may supervene, the most important of which are temperature and nourishment, but the most profound influence on basic activities is that of the sun, from the energy of which all life is ultimately derived.

The pattern of the *flowering of many plants* is a good example of this general tendency—and an important one, for floral initiation is a fundamental factor marking the change from vegetative life to reproductive activity. Although experimental work of considerable merit had been done on the effects of artificially varying the periods of illumination on the growth and maturation of plants, particularly by Schübel (1880) in England, Tournais (1912) in France, and Klebs (1918) in Germany,² it was left to two American botanists, Garner and Allard (1920), to establish finally the important fact that in many species flowering did not depend primarily on temperature or the intensity of illumination but on *the daily lengths of the periods of light and darkness*; they therefore introduced the term **PHOTOPERIODISM**. In many plants the determining factor is the length of the day, and, as was first proved by the Russian botanist, Cailahian (1936), the primary receptor organ is the leaf; even although the rest of the plant is covered, the exposure of one leaf, or even part of a leaf, to the rhythm of light and darkness determines the cycle, and if the leaves are removed and the plant rendered naked to live on its stored food it immediately becomes

¹ See Grossenbacher (1939), Engel and Heimann (1949), Flügel (1949), Hagan (1949), Heimann (1950–52), Enderle (1951), Vegis (1955), Bünning (1956), Wareing (1956), and others.

² For review, see Smith, 1933.

indifferent to the alternating change between darkness and light. Moreover, if a plant of one type is denuded of leaves and the leaf of a plant with a different cyclic character is grafted onto it, the host-plant assumes the periodicity of the grafted leaf.¹

Two different responses are well recognized. In summer-flowering plants (*long-day plants*) which bloom when the spring days lengthen, the formation of

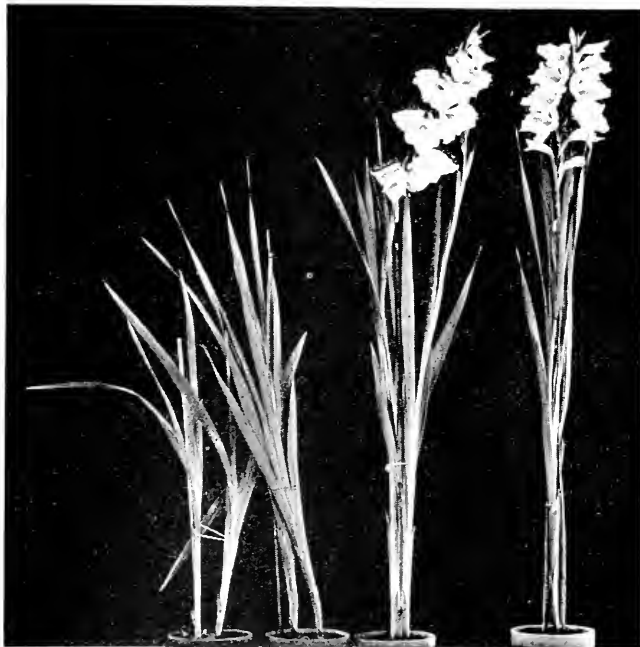


FIG. 7.—THE EFFECT ON FLOWERING OF INTERMITTENT LIGHT DURING THE NIGHT.

On the left are two gladioli (*long-day plants*) grown in a control greenhouse with a normal solar day-and-night rhythm; on the right, two similar plants grown with intermittent light during the night (Boyce Thompson Institute for Plant Research).

flowers is inhibited in darkness while during the periods of light some substance is presumably formed in the leaves which counteracts this inhibition; in *short-day plants* which come to flower when the autumn days shorten, both dark and light periods are necessary for the development of the stimulus, each with opposite effects, one depending on light-energy and the other being inhibited by light. In summer-flowering plants artificial light during the night promotes flowering (Fig. 7); in autumn-flowering plants flowering in short days, light during the day promotes flowering but short periods of light during the night prevent it.

¹ Melchers (1936-37), Cailahian (1936-47), Loehwing (1938), Borthwick and Parker (1938-40), Hamner and Naylor (1939), Harder and v. Witsch (1940), Withrow *et al.* (1943), and others.

The mechanism of these photoperiodic responses is unknown but several facts are now established. It is significant that a brief exposure (1 sec. in some species) to light of a very low intensity (of the order of 1 ft. candle, that is, of the intensity of moonlight) is sufficient to determine the periodicity. The wave-length of the light is of importance, for the action-spectrum shows a specificity with maxima in the red and blue—a fact which suggests the presence of one or more absorbing pigments; moreover, there are indications of an antagonism between the action of different spectral regions, while near infra-red radiation takes an active part in the effect (see Wassink and his co-workers, 1950–56). Such a pigment (or pigment-mixture) has not been isolated, but Borthwick and his colleagues (1948–54) speculated that it is an open-chain tetrapyrrol pigment, a distant relative of chlorophyll. With its aid a photosynthetic reaction takes place, the nature of which is unknown¹ with the probable result that one or more plant hormones,² perhaps both activating and inhibiting in their action, travel down the leaf-stalk and up the shoot to influence flowering; the substance can travel through living cells and across grafts but not across an inanimate obstacle (Cailahian, 1940).

The fact that such a substance (or substances) has eluded chemical detection, has stimulated several alternative hypotheses.³ However that may be, and whatever the intimate mechanism, the fact remains that the order of the procession of flowers through the seasons is largely determined by the diurnal periodicity of light and darkness.

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¹ Review, see Lang, 1952. ² p. 39.

³ See Bünning (1937–50), Bonner and Thurlow (1949), Bonner (1949), Harder and van Senden (1949), van Senden (1951). Recent research indicates that the gibberellins are of fundamental importance in the photoperiodism of plants.

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PHOTOPERIODISM IN ANIMALS

DIURNAL METABOLIC RHYTHMS are equally remarkable among animals, for the cycle of day and night with its rhythm of changes in illumination, temperature and other environmental factors has so impressed itself upon living creatures in the course of their palæontological development that many of their metabolic processes vary with a corresponding periodicity, synchronized as it were by an internal physiological clock.

These physiological rhythms have received much study and have accumulated a considerable literature.¹ Among Mammals, including Man, the periodicity of *sleep and activity* is the most obvious,² possibly a survival of the nocturnal reduction of nervous activity in primæval Amphibians. Most animals are diurnally active; but in nocturnal animals the cycle of activity is reversed.³ A similar cyclic variation is seen in bodily *temperature*.⁴ In Man the temperature through the day is higher than at night, but considerable variations occur in the characteristics of the curve; in some individuals the peak is in the morning, in others in the afternoon and in others at an intermediate time. The *blood constituents* show a variation affecting the hæmoglobin, hæmatocrit readings and plasma proteins,⁵ while the variation in the eosinophil count is dramatic; in Man, in the morning there is an eosinopenia⁶; in nocturnal animals such as mice the count is high in the morning and low in the early hours of the night.⁷ A similar rhythm acting independently of the intake of fluid affects the *urinary output*, involving not only the excretion of water but also that of electrolytes (Na, K and chlorides, etc.) and urea which persists even if the 24-hour day is disrupted for periods up to 6 weeks.⁸ Even more fundamental cellular processes are involved such as *mitotic activity* which is maximal in the rest-period at

¹ See Kleitman (1949), Menzel (1952), Halberg (1953), Harker (1958).

² See Kleitman (1939).

³ Rat—Richter (1922), Browman (1937); wood rat—Colton (1933); vole—Davis (1932); hedgehog—Herter (1934); mice—Achelis and Nothdurft (1939), Aschoff (1952), Kowalski (1955); wild mice—Johnson (1926).

⁴ See Kleitman *et al.* (1937-38), Kleitman (1949), Halberg *et al.* (1953).

⁵ Renbourn (1947).

⁶ von Domarus (1931).

⁷ Halberg and Visscher (1950-52).

⁸ Gerritzen (1936-40), Mills (1951), Mills and Stanbury (1952), Mills *et al.* (1954), Lewis *et al.* (1956), Lewis and Lobban (1956).

midnight and minimal at noon, a rhythmic variation first noted in plants¹ and discovered in mammalian tissues (including the corneal epithelium) by van Leijden (1917), confirmed in the human epidermis by Cooper (1939) and noted in the cornea of tadpoles by Meyer (1954).² It is interesting that it is a physiological process not seen in cancer cells. As will be fully discussed in a subsequent volume, a diurnal variation of some 3–5 mm. Hg occurs in the *ocular tension*.³

Established by constant repetition, these rhythms persist for some time in the absence of environmental reinforcement when the external rhythm has been artificially altered or has ceased. The mechanism of these changes is unknown; most of them are probably maintained by rhythmic changes of activity in the neuro-vegetative centres of the diencephalon, while the endocrine system, particularly the pituitary

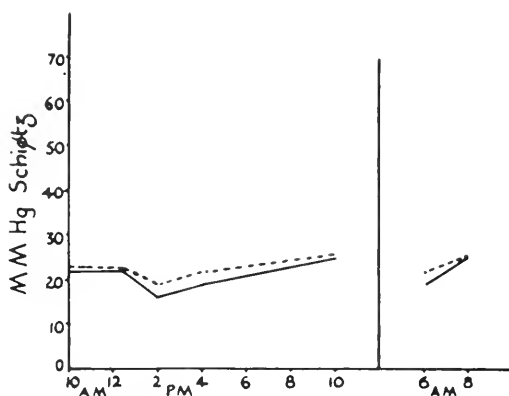


FIG. 8.—THE NORMAL DIURNAL VARIATION IN THE INTRA-OCULAR PRESSURE.

The abscissæ are times of the day; the vertical line denotes when the patient was asleep.

complex, probably has some effect. Apart from the long-known centres controlling thermo-regulation and urinary output, functions such as the variation in circulating eosinophils are governed by the diencephalo-hypophyseal system through the secretion of corticosteroids by the adrenal cortex (Hume, 1949; Porter, 1953), and the evidence is rapidly accumulating that a region in the same neighbourhood exerts control over the intra-ocular pressure (v. Sallman and Lowenstein, 1955; Gloster and Greaves, 1957). However they are controlled, these rhythms are real and autochthonous. Thus in man the normal variation in temperature persists for a considerable period after the commencement of habitual night work, and the diurnal rhythm of urinary flow survives a uniform intake of fluid throughout

¹ Kellicott (1904).

² See Blumenfeld (1939), Halberg (1953).

³ Maslenikow (1904); see Duke-Elder (1952). See also p. 560.

the 24 hours and the reversal of the sleep habit. Similarly, the normal phasic swing of the ocular tension is independent of the blood pressure, osmotic changes in the blood, illumination, the time of meals, feasting or fasting, or bodily activity; the rhythm can only be altered by a complete reversal of the sleep habit established over some time (Raeder, 1925) (Fig. 8). The fact that such rhythms as the diurnal variation in temperature in the new-born infant, or the 24-hour periodicity of activity of the newly hatched chick kept under constant laboratory conditions (Aschoff and Meyer-Lohmann, 1954), are apparent from birth indicates that at any rate some of these fluctuations are fundamental and innate—an environmental influence of biological value which has with time so impressed itself upon organisms that it has become hereditarily transmitted.

Some of these diurnal variations, however, seem to depend on environmental stimulation. Thus the cyclic variation in the eosinophil count of mice was found by Halberg and his associates (1954) to be abolished by the enucleation of both eyes, although it partially returned some 5 months after blinding. The rhythm of diurnal activity of the minnow, *Phoxinus*, is said to be reversed on blinding (Jones, 1956). In man the variation in eosinophilia depends to some extent on activity (Halberg *et al.*, 1953), and illumination has a subsidiary influence (Appel and Hansen, 1952; Landau and Feldman, 1954).

The same *rhythms in general activity* are seen in Invertebrates, among which Insects provide some of the most dramatic examples (see Welsh, 1938; Wigglesworth, 1953). The habit of nocturnal activity and diurnal catalepsy shown by the stick-insect, *Dixippus*, for example, persists unchanged for some days in permanent darkness or in reversed illumination (Steiniger, 1933), a daily rhythm which applies to such activities as defaecation and oviposition (Kalmus, 1938). The same general tendency is seen in many other species.¹ The rhythm may, indeed, be acquired in the larval stage in response to diurnal changes of light, persist through the pupal stage and determine the activity in the adult.² A metabolic rhythm in which the CO₂ is higher (sometimes by 30%) during the night even although the animal is kept in constant darkness is seen in Crustaceans.³ A similar diurnal rhythm of the opening and closing of the valves of the clam, *Venus mercenaria*, persists under laboratory conditions of constant illumination; it is interesting that in this case there is also a persistent tidal rhythm and the interaction of the two produces a lunar cycle (Bennett, 1954). A similar phenomenon whereby an endogenous tidal rhythm displaces

¹ It is seen in some forest insects (Lutz, 1932; Park and Keller, 1932), mayflies (Harker, 1953), cockroaches (Gunn, 1940; Mellanby, 1940; Harker, 1954), millipedes (Park, 1935), and other species.

² In *Leptinotarsa*—Grisson (1943).

³ The crab, *Carcinus*—Henkes (1952); the woodlouse, *Oniscus*—Cloudesley-Thompson (1952).

the endogenous diurnal rhythm, is seen in the fiddler-crab, *Uca* (Brown *et al.*, 1952-54) and also in marine forms of the protozoon, *Euglena* (Pohl, 1948). A lunar as well as a diurnal rhythm of activity and oxygen consumption is seen in the earthworm, *Lumbricus* (Ralph, 1957), and in crayfish such as *Cambarus virilis* (Guyselman, 1957). The timing of these rhythms with respect to the solar day when the animals are kept in darkness has been altered by lowering the temperature (the fiddler-crab, *Uca*, Stephens, 1957).¹

THE SEXUAL CYCLE OF ANIMALS, as with flowering in plants, is also frequently determined by the influence of light as expressed by the gradual change in the length of day in the annual solar cycle ; in this way the onset of the breeding season becomes rhythmic as though there has been implanted on the central nervous and hormonal systems a pattern of behaviour automatic and innate so that it can only be altered experimentally by a prolonged disturbance of the natural phases. In some species, it is true, particularly in Invertebrates and the lower Vertebrates, other factors such as temperature and humidity also enter into the question, but controlled experiments have shown that these and other extraneous circumstances, such as physical activity and feeding, are often secondary and in many cases can be excluded and that the most important factor is the *duration* of the period of light—not its intensity or wave-length. These phenomena have been particularly studied in animals inhabiting the northern hemisphere. Spring in these regions with its increasing days is the appropriate season for reproduction if survival is to be maintained, and in those species with a long gestation period, the shortening days of autumn are most suitable for mating. In general, when species with a breeding periodicity of this type are experimentally subjected to artificially lengthening days in late autumn or winter, they can be brought from their sexually quiescent condition into the ripeness typical of spring, while conversely, if the lengthening days of spring are artificially curtailed, sexual regression occurs ; indeed, it is possible by these means to bring some types (birds, for example) into breeding condition several times in the year—a change which applies not only to anatomical considerations such as the development of the gonads, but also to those habits and modes of conduct which are essentially sexual in origin such as (in birds) singing and migration.

Such phenomena have been investigated in many species of Invertebrates, Fishes, Amphibians, Reptiles, Birds and Mammals.

In the INVERTEBRATES, even among Protozoa, Ehret (1951) found that the diurnal rhythm of the mating reaction of *Paramaecium bursaris* persists for several days in complete darkness and can be altered by varying the illumination

¹ Compare p. 22.

at different periods of the daily cycle. In snails, a prolongation of the diurnal period of light beyond 13 hours stimulates egg-laying, while periods of 11 hours or less inhibit it (Jenner, 1951); it is interesting that short intervals of illumination during the dark periods of a short-day cycle stimulate egg-laying, showing that, as with short-day plants, the length of the dark period is an essential feature in the stimulus. Similarly the strawberry-root louse, *Aphis forbesi*, can be made to breed in midsummer instead of February by artificially curtailing the summer days (Marcovitch, 1923). A more dramatic influence is seen in the plant-louse, *Psylla*: individuals hatched in autumn differ from those hatched in spring but the winter-type can be produced in spring by subjecting the larvae to an artificial diurnal rhythm in which the period of light is shortened (Bonnet-maison and Missonnier, 1955).

Among FISHES, temperature has been shown to be a potent factor, but it has been demonstrated that the reproductive cycle of the trout can be photo-periodically determined (Hoover and Hubbard, 1937); similarly the activity of the gonads of certain AMPHIBIANS such as the clawed toad, *Xenopus laevis*, (Shapiro and Shapiro, 1934) and REPTILES such as the lizard, *Anolis carolinensis* (Clausen and Poris, 1937), has been altered by means of artificial illumination.

BIRDS show more dramatic changes than most species, and these have received much attention probably because of their obvious habits of migration and singing, the sexual connection of which has been recognized since the time of Aristotle. For long the annual rhythm of the avian gonad was held to be determined by temperature. It is true that in the old custom of "muit" long prevalent in Holland, birds were brought into song in autumn by confining them in the dark in the middle of June and exposing them to light in September, and that by the similar ancient practice of "yogai", Japanese pet birds were brought into singing condition in January by providing them with extra hours of illumination in the autumn (Miyazaki, 1934). In this respect, however, zoologists waited on botanists; for although Schafer (1907) had suggested that migration, because of its accurate periodicity, must depend on the mathematically regular changes in length of day rather than on the notoriously irregular variations in climate, it was not until the work of Garner and Allard on the influence of photo-periodism on the flowering of plants had been published in 1920¹ that Eifrig (1924) propounded a similar hypothesis to explain the habits of birds, a conception eventually proved by the experimental work of Rowan (1925-38).

Rowan's classical work was on the junco finch, which migrates from wintering grounds in the middle United States to Alberta; he found that even if the birds were retained in an aviary in Alberta, provided they were subjected to the artificial increase of daily illumination (2-3 mins.) that they would have experienced in the early spring in the States, their gonads matured and they burst into song in December despite the temperature of the Canadian winter (minimum, -50° F). These results were confirmed by Bissonnette (1930-32) in Connecticut experimenting on starlings; and it is now amply established that among many birds of the temperate zones of the northern hemisphere, the testes of which normally reach a peak of activity as the days lengthen in late spring, an artificial increase of the period of illumination over some time brings on a precocious activity, while a curtailment or denial of light brings on the reverse changes.² On the other hand, confinement of male parrots in continuous

¹ p. 10.

² See among others: junco, *Junco hyemalis*—Rowan (1929), Jenner and Engels (1952); starling, *Sturnus vulgaris*—Bissonnette (1930-32); pheasant—Martin (1935), B. C. Clark *et al.* (1936-37); house sparrow, *Passer domesticus*—Riley (1936), Kirschbaum and Ringoen (1936); white-throated sparrow—Jenner and Engels (1952);

darkness for a month results in testicular activity, while continuous illumination produces a resting state (Vaugien, 1952). The same result follows a "natural" change in the day-night cycle, for if the birds in the northern hemisphere are transported to the southern, their breeding season is reversed (Rowan, 1926); while in regular migrants across the equator the stimulus for the recrudescence of sexual activity and enlargement of the gonads is the shortening of the days in March in southern lands (Rowan, 1938), an inherent habit which can only be broken if such species are retained for several years in the southern hemisphere and prevented from migrating (Marshall, 1937; Baker and Ranson, 1938). It would therefore seem established that the sexual cycle and the migration of birds, rhythms which have become innate, are determined essentially by photoperiod, although it is to be remembered that periods of darkness may have an influence equal to or even more potent than light (Hammond, 1953; Kirkpatrick and Leopold, 1953), while temperature also has an adjuvant effect (Bissonnette, 1937; Farner and Mewaldt, 1952-53; Wilson *et al.*, 1956).

Similarly among MAMMALS, male ferrets,¹ mice² and ewes³ can be brought into œstrus in winter when normally they are in anœstrus by subjecting them to rhythmic periods of increased illumination for 2 months or more, while the gonads of the field-mouse have been shown to diminish by exposing the animals to increased periods of darkness (Baker and Ranson, 1932).⁴ As would be expected, these changes do not apply to non-seasonable animals⁵ or those that reach sexual maturity during hibernation⁶ or aseasonation.⁷ Among those animals in which it is operative, however, and particularly among those with migratory habits, the periodic behaviour thus induced sometimes assumes legendary exactitude, a fact commented on since the days of Pliny; the cuckoo arrives in England on "Cuckoo Day", the early stream of swifts is expected to arrive on the last three days of April and the big arrival on May 24th, while in the late autumn each year the male markhor is said to descend from the high Hindu Kush into the valleys to meet the females on December 14th precisely, and the rut begins (Burton, 1951).⁸

The mechanism of the action of light in these photoperiodic activities varies, but in general is mediated through hormones the activity of which is largely determined by stimulation through the eyes. This complex matter will be discussed subsequently,⁹ but at this stage it is convenient to note that in Crustaceans, several hormones are

white-crowned sparrow—Farner *et al.* (1953); dove, *Zenaidura macroura*—Cole (1933); Japanese white-eye, *Zosterops*—Miyazaki (1934); duck—Benoit (1934-35), Radnót (1953-55); quail—B. C. Clark *et al.* (1936-37), Hammond (1953); fowl—Radnót (1955), Radnót and Orbán (1956).

¹ Bissonnette (1932), Marshall and Bowden (1934-36), Hart (1951), Thomson (1954).

² Whitaker (1936).

³ Hafez (1951).

⁴ For further details of the mechanism involved, see p. 559.

⁵ Guinea-pigs—Dempsey *et al.* (1933-34); rabbit—Smelser *et al.* (1934).

⁶ Squirrel—Wells (1934-35), Johnson and Gann (1933).

⁷ Alexander and Bellerby (1935-38), Bellerby (1938).

⁸ In a similar manner the palolo (Polychæte) worms of the South Pacific shed their eggs or sperms in countless millions, sufficient to give the sea the appearance of vermicelli soup, at a specific time. These are eminently edible, and the natives of Samoa have learned to expect a great feast precisely at dawn one week after the November full moon.

⁹ p. 547.

secreted in the eye-stalks and central nervous system and stored in the sinus glands and these regulate ovarian maturation and testicular development. In Vertebrates the pituitary gland exerts an analogous gonadotropic influence under the control of its associated centres in the diencephalon which in turn receive their stimulation from the retina.¹

PHOTOPERIODISM IN PIGMENT MIGRATION. Pigment, the function of which is so closely related to light, would be expected to be peculiarly susceptible to its influence ; in its migration to cause colour changes,² rhythmic diurnal variations of a primitive type frequently survive. That a persistent rhythm of this kind occurs in the *migration of the retinal pigment* ³ in the eyes of a noctuid moth, *Plusia gamma*, was first reported by Kiesel (1894), an observation which has been repeated in several Arthropods with compound eyes and shown to persist even although the animals are kept for a considerable time in conditions of constant illumination and temperature or are reared from the larval stage in the laboratory in constant darkness.⁴ The effect is well seen in the crayfish in the eye of which there is a tapetal reflecting pigment ⁵ obscured during the day but unprotected at night so that the eye then assumes an orange glow ; even if the animal is kept in conditions of constant darkness and temperature, the diurnal rhythm of orange "eye-shine" at night will continue automatically for months (Welsh, 1941). Similar rhythms affecting the retinal and tapetal pigments are seen in many species of Crustaceans (Henkes, 1952), and it would appear that these pigmentary movements are under hormonal control, a subject which will be discussed in a later chapter.⁶

Closely associated with the movements of the retinal pigment are the corresponding *movements of the rods and cones* of some of the lower Vertebrates. As with the retinal pigment, these movements are usually a direct response to light, but evidence was produced by Welsh and Osborn (1937) that these elements in the eye of the catfish underwent a diurnal rhythmic change of position even although the fish were kept in constant darkness ; the mechanism of this rhythmic activity is unknown.

The *integumentary chromatophore system* frequently shows similar cyclic activities. The responses of this pigmentary system to light are complex and will be studied in a later section ⁷ ; it is sufficient to note here that many animals show a rhythmic day-night change of colour wherein they pale by night and darken by day, a rhythm which may persist for a considerable time if they are kept in conditions of constant

¹ p. 556.² p. 82.³ p. 170.

⁴ In the beetle, *Bolitotherus cornutus*—Park and Keller (1932) ; and a number of Crustaceans such as fresh-water shrimps, *Macrobrachium* and others—Welsh (1930) ; crayfish, *Cambarus*—Bennett (1932), Welsh (1939-41) ; crab, *Uca*—Smith (1948) ; Brown *et al.* (1951-54), Kleinholz (1937) ; and so on.

⁵ p. 165.⁶ p. 547.⁷ p. 82.

illumination or darkness.¹ Gamble and Keeble (1900) first reported such a cyclic diurnal colour change which persisted under constant illumination in the prawn, *Hippolyte varians*, but although subsequent work has not confirmed this particular observation (Kleinholz and Welsh, 1937), the phenomenon has been demonstrated in a number of species of both Invertebrates and the lower Vertebrates.² In some cases these diurnal changes are largely masked by other factors such as pigmentary changes adopted to mimic the background,³ but the

FIGS. 9 AND 10.—DIURNAL RHYTHMS IN THE PIGMENT OF THE CRAB, *UCA*.

The black and white segments at the top of the graphs and in the corresponding position immediately below the graphs represent the normal rhythm of daylight and darkness. The second tier of markings below indicate the experimental variations introduced. Ordinates: the degree of pigmentation expressed in Hogben and Slome's scale, 1 representing complete concentration of pigment, *i.e.*, the light phase, and 5 its complete dispersal, *i.e.*, the dark phase (Brown and Webb, 1949).

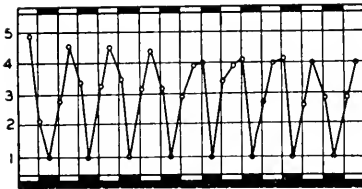


FIG. 9.—The normal diurnal rhythm of pigmentation (dark through the day and light at night) is seen to continue uninterruptedly after the animal has been 9 days in darkness.

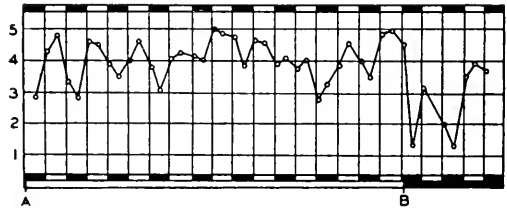


FIG. 10.—At the beginning of the experiment *Uca* was exposed to continuous illumination (80 foot candles) from A to B. There is a decrease in amplitude and then a gradual inhibition of the rhythm until eventually the chromatophores change irregularly. At B the animals were transferred to continuous darkness, whereupon the chromatophores became almost completely concentrated and thereafter a normal 24-hour rhythm in phase with solar day-night was observed.

effect of the underlying rhythm is seen in the increased rapidity of these secondary responses when they are in phase with the primary diurnal cycle and their sluggishness when they antagonize it. In other animals the fundamental rhythm is preponderant so that secondary

¹ 8 to 9 weeks in the beach-louse, *Idotea*—Menke, (1911); 18 days in the lizard, *Anolis*—Rahn and Rosendale (1941); and so on.

² Several Invertebrates such as the black sea-urchin, *Diadema antillarum*—Millett (1950); many Crustaceans in addition to *Idotea*: the prawn, *Palaemon*—Keeble and Gamble (1904), the fiddler crab, *Uca*—Abramowitz (1937), the Isopod, *Ligia*—H. Smith (1938); a few Insects such as the stick-insect, *Dixippus*—Schleip (1910). Compare, for example, Figs. 64–68.

A number of Vertebrates, particularly in their youth (Cf. Figs. 70 and 73); Cyclostomes such as the lamprey, *Lampetra*—Young (1935), Jones (1955); Amphibians such as salamander larvae and frogs—Hooker (1914), Welsh (1938); and Reptiles such as the American horned "toad", *Phrynosoma*—Redfield (1918), the lizard, *Anolis*—Rahn and Rosendale (1941), and the chameleon—Zoond and Eyre (1934).

³ p. 82.

environmental factors have but a slightly modifying effect upon it. A good example of this is the crab, *Uca*, the responses of which have been extensively studied¹; the diurnal rhythm of its colour change is remarkably constant, and within wide limits is independent of influences such as humidity and temperature, but the influence of metabolism on the phenomenon is exemplified in its retardation with a lengthening of the cycle on exposure to cold below 6° C (Figs. 9 and 10).

This rhythmic mechanism operating to disperse pigment in the day phase and concentrate it in the night phase of the cycle would seem to be adaptive in function, partly protective against deleteriously bright illumination, partly thermo-regulatory. In all species in which these colour changes occur the controlling factors are hormones differing in nature from the retinal pigment hormones but, like them, elaborated in Invertebrates by the neuro-secretory system and in Vertebrates by the neurohypophysis both of which show an endogenous rhythm. This question will be discussed in a subsequent chapter.²

The seasonal changes in colour of the coats of many Birds and Mammals are analogous phenomena which are also to some extent determined by photoperiod. It is well known that the majority of common birds undergo a post-nuptial moult immediately after the breeding season and a second pre-nuptial moult in spring when they assume their wedding robes. The times at which birds assume their nuptial and winter plumages are governed by a number of factors, the most potent of which is a pituitary hormone with an inherent cyclic activity depending in part on the length of the daily light periods (Witschi, 1935; Brown and Rollo, 1940; Lesher and Kendeigh, 1941; Kobayashi and Okubo, 1955). A similar control operates the seasonal moulting of many northern Birds and Mammals the colours of which change from a summer brown to a winter white.

Among Birds, the ptarmigan of the northern tundra or the high mountains (Höst, 1942), and among Mammals the varying hare (Lyman, 1943) and the ermine (Bissonnette and Bailey, 1944) are good examples of this; these phenomena of moulting and change of colour can be induced out of season by artificially varying the diurnal periods of illumination. It is interesting that in the hare the eyes seem to be the normal receptors of this stimulus since if these are masked the changes do not occur. The pituitary seems to be the only endocrine gland involved since castration and thyroidectomy in the hare are without effect (Lyman, 1943), while hypophysectomy abolishes the cyclic moulting of ferrets (Bissonnette, 1935-38).

PHOTOPERIODICITY IN BIOLUMINESCENCE. The ability to produce light occurs widely but sporadically among bacteria, fungi, and most types of animals

¹ Abramowitz (1937-38), Brown and Webb (1947-49), Brown and Sandeen (1948), Webb (1950).

² p. 547.

from the Protozoa to the chordate Fishes ; it is a phenomenon which will be discussed in greater detail later.¹ It is well known that in most animal species the reaction appears intermittently in response to various stimuli, light having a general inhibitory effect, sometimes directly by destruction of the photogenic material in the light-producing cells, sometimes indirectly, acting through a central regulatory mechanism, hormonal or nervous (Harvey, 1925 ; Heymans and Moore, 1925 ; Moore, 1926). In the present connection it is interesting to remark that in a number of species there is a daily rhythm in the capacity to luminesce, a phenomenon seen even in unicellular Dinoflagellates (Harvey, 1952); and in some types of Insects² and perhaps in some jellyfish³ and a balanoglossid⁴ the rhythm may persist for several days so that the animal will light up at the normal time of the day even if kept in constant darkness.

A final expression of DIURNAL RHYTHMICITY is seen IN THE TIME-MEMORY OF SOME ARTHROPODS AND BIRDS. This curious and interesting phenomenon was first demonstrated in bees by von Stein-Beling (1929-35) who showed that within a cycle of 24 hours bees could be trained to visit an artificial feeding station at regular occasions throughout the day, a habit which could not be maintained if an attempt were made to operate within a cycle greater or less (e.g., 19 hours) than the normal solar diurnal rhythm. This ability has since been verified by a number of observers⁵ and it has been confirmed in wasps⁶ and ants⁷ as well as in the Amphipod *Talitrus*.⁸ So far as honey-gathering insects are concerned it is probably connected with the hours at which flowers periodically offer their nectar, but other activities are also involved. Thus Kalmus (1935) found that if larvæ and pupæ of *Drosophila*—an insect which normally emerges from its pupa before dawn—were kept in darkness during the daytime and artificially illuminated for 3 consecutive nights, the flies emerged in the evenings, remembering the time of the artificial dawn even although kept in perpetual darkness. Such time-keeping mechanisms or “internal clocks” are of wide occurrence, keeping time automatically with considerable precision, but regularly set and kept in pace by light stimuli. It would seem that the rhythm is influenced metabolically since it can be retarded by low temperatures (under 5° C, Kalmus, 1934) or by drugs ; thus Grabensberger (1934) found that by feeding quinine to trained bees, arrival at the sources of food was retarded, while it was accelerated by iodothyroglobin.

A similar apparently innate time-sense can be demonstrated in some Birds, which we will see⁹ assumes considerable importance in their extraordinary ability to navigate over long distances. Thus Stein (1951) found that passerine birds could be trained to come to feed at a particular hour each day provided only that a 24-hour cycle were maintained, an acquirement retained for some considerable time although the birds were kept in constant illumination or had irregular feeding times ; experimental exposure to irregular periods of light and darkness, however, tends to disorientate this sense when it is used as an aid to navigation (Matthews, 1953-55).

¹ p. 736.

² Such as the firefly, *Photinus*—Buck (1937).

³ *Pelagia*—Heymans and Moore (1924-25).

⁴ *Ptychodera*—Crozier (1920).

⁵ Wahl (1933), Kalmus (1934-54), Kleber (1935), v. Frisch (1937), and others.

⁶ Verlaine (1929).

⁷ Grabensberger (1934).

⁸ Pardi and Papi (1952-53).

⁹ p. 63.

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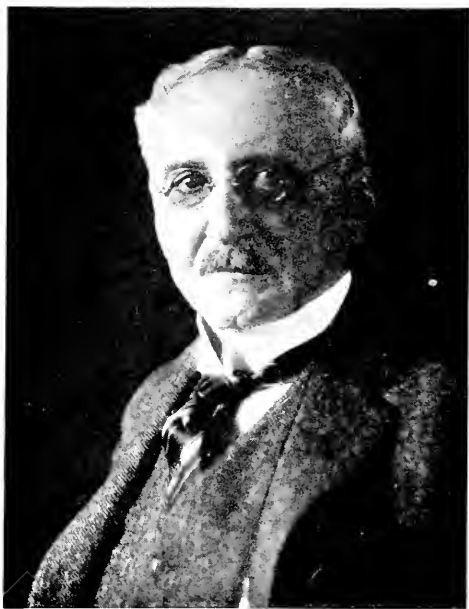


FIG. 11.—JACQUES LOEB (1859–1924).

JACQUES LOEB was assistant in physiology at the University of Würzburg where he was much influenced by his botanical colleague, Sachs ; he then went to Strasbourg, and thereafter, going to America, became professor of physiology at the Universities of Chicago and California, and finally head of the Division of General Physiology at the Rockefeller Institute for Medical Research in New York. I am indebted to that institution for his photograph. SAMUEL O. MAST, Professor of Zoology in Johns Hopkins University, was one of the band of men who have made Baltimore outstanding among the centres of learning in the world.

It is good to have Jacques Loeb and Samuel Mast on the same page—the two great protagonists of the mechanistic and the vital interpretations of animal behaviour, both of whom propagated their views with unusual vigour—the first an intellectual descendant of Descartes, the second of Leibnitz and Goethe.



FIG. 12.—SAMUEL O. MAST (1871–1947).

CHAPTER III

THE EFFECT OF LIGHT ON MOVEMENT

THE control of the movements of living organisms, both plants and animals, by light is a fundamental function of great phylogenetic age, preceding the acquirement of vision and, indeed, leading directly to its development¹; it will be remembered that the association of the functions of equilibration and orientation with the visual system of the higher animals is in every sense basic. This primitive control of movement by light is undoubtedly an adaptive process, directing the organism to regions in the environment which are favourable to it, and has originated and evolved in the same way as other biologically useful reactions.

Historical development

It was originally held that the orientation of primitive organisms in space depended on the exercise of those "vital forces" the presence of which were considered to differentiate living creatures from the inanimate world; and it was not until the time of the Cambridge clergyman-journalist, John Ray (1693), that a mechanistic explanation was offered to account for this aspect of the behaviour of plants. This English botanist suggested that plants placed before a window turned towards the light because the side towards the window was cooler than that towards the room and consequently grew more slowly so that the plant became bent by the relatively greater growth on the warmer side. The Huguenot botanist, August de Candolle (1832), on the other hand, introduced the conception that light rather than heat was the responsible agent, a concept elaborated and rationalized by Sachs (1882), the botanist of Würzburg; he maintained that orientation was determined by the directional incidence of the light and so formulated the interpretation of these phenomena generally current today.

Meantime, similar reactions in the animal world were considered to be dominated by a vital force usually conceived as acting automatically and thoughtlessly, a view epitomized by the great French philosopher, René Descartes (1650). The publication of Darwin's *Origin of Species* in 1859, however, caused a revolution in biological thinking so that contemporaneous writers spent much ingenuity in interpreting the behaviour of the lower animals in an anthropomorphic² way, attributing their reactions to primitive psychic activities which

¹ p. 105.

² ἄνθρωπος, man; μορφή, form.

were held to be pre-human in the sense that they were the evolutionary forerunners of the mental attributes of man.¹ Emotions were thus attributed to the lowest animals so that their conduct could be equated to that of man who was their descendant. The rationalization of zoology thus lagged behind that of botany, the progress of which seems to have been unnoticed by those engaged in the study of animal life, possibly because the temptation to endow plants with anthropomorphic attributes was less compelling.

In extenuation of the general acceptance of what would be considered a shallow philosophy today, it must be remembered that the doctrine of "animal spirits" was of extreme antiquity²; as a basis of his philosophy man required the concept of an incorporeal essence to give meaning even to corporeal objects, a need still felt by such philosophers as Descartes (1650-64) and such scientists as Willis (1670) and Boerhaave (1708); and it was not until almost the middle of the 19th century that the physical discoveries of Galvani (1791), the anatomist of Bologna, and Volta (1796-1800), the physicist of Pavia, were applied to the reactions of living creatures by the two great founders of modern physiology, Johannes Müller (1834) and du Bois-Reymond (1843-49), who laboriously began to build up a physiological doctrine on a physical basis. Almost half a century was to pass, however, before these new concepts, already accepted by botanists and for long part of physiological teaching, were applied to the problems of the orientation of animals by light and other stimuli. The early experimenters in this field from Paul Bert (1869) to Graber (1883-84) interpreted these reactions in anthropomorphic terms: animals sought or avoided light because it was "agreeable" or "disagreeable"; indeed, the experimental studies of Engelmann (1879-82) and Verworn (1889) were the first in which attempts were made to place a physiological interpretation upon these responses, attempts which rapidly fructified so that the doctrine soon became generally accepted by zoologists and physiologists.³

At the beginning of this period of activity and reorientation, a prophet arose in the person of the German biologist, JACQUES LOEB (1859-1924) (Fig. 11). Loeb's life-work was a study of the differentiation between the animate and the inanimate and his thesis the identity of the two, for to him all living things were chemical and mechanical

¹ Darwin (1872), Lubbock (1881-89) in England; Paul Bert (1869), Plateau (1886), Binet (1894) in France; Graber (1883-84) in Germany; Romanes (1883) in America; and others.

² This belief permeated the whole of ancient thought and mythology. Even although the philosophy of the Ionian Greeks became more impersonal than the bronze-age cosmologies, Thales of Miletus, c 625-545 B.C., the first of the Greek natural philosophers, ascribed a soul to the lodestone because it could move a piece of iron, a view generalized by Anaxagoras, c 488-428 B.C., who ascribed all motions of material or living things to the operation of a mind or a soul. Erasistratus of Chios, fl. c 300-260 B.C., believed that the inspired air was transferred into vital spirit in the heart, to be relayed as such all over the body by the arteries; the small amount reaching the brain was again transformed into animal spirit (*animus*, a soul) which was distributed by the nerves and was responsible for sensitivity and movement. The same philosophy was further associated by Galen, A.D. c 130-200, and for centuries was an accepted doctrine.

³ Loeb (1913), Jennings (1904-6), Mast (1906-38), Bohn (1909), Patten (1919), and others.

machines the activities of which were explicable by the same physical laws.¹ As a young colleague of the botanist, Sachs, at Würzburg, he appreciated the immense strides his friend had made in the interpretation of the responses of plants and unicellular organisms to light, and applied the same techniques to the animal world. All voluntary and instinctive reactions of animals he considered to be determined by internal and external forces, the majority of their responses thereto depending upon their bilaterally symmetrical structure. Thus, in the simple reaction of an animal going towards or away from a light, if the velocity of the chemical reactions in one eye is increased, the equality of "tonus" in symmetrical muscles on the two sides of the body is altered so that the animal is compelled to change its direction of locomotion; as soon as the plane of symmetry becomes directed through the source of light, muscular tone becomes equalized and the animal progresses straight ahead until some other asymmetrical disturbance changes its direction of motion. Any other form of energy, he claimed, acted in the same way as light, so that the animal, which may appear superficially to move purposively and of its own will, is in reality forced to go where it is carried by its legs or wings. Animal conduct was thus interpreted as consisting of forced movements, a conception very different indeed from the anthropomorphic and teleological views prevailing throughout the nineteenth century.

Loeb pursued his theories with immense activity and application, and defended them with unusual vigour and stubbornness. It soon became obvious, however, despite his warm advocacy, that the intricacies of animal behaviour could not be contained within a theory so simple. Moreover, its all-embracing character and its rigidity readily opened it to attack as observations on the complexity of the conduct of animals multiplied. Jennings (1904-6) first showed that the reactions even of Protozoa could not be explained in this deceptively simple way, and the automaticity of the reactions of animals was challenged and disproved by many workers,² but by none more conclusively and consistently than by SAMUEL O. MAST (1871-1947) who proved to be Loeb's most violent and successful opponent (Fig. 12). Undoubtedly Loeb had swung the pendulum too far. A considerable reconciliation between the two opposing views was put forward by Kühn (1919), but general accord has by no means yet been reached.

It is probably true that the mechanical evidences of organic activities ultimately conform to the rules of chemistry and physics; *but these rules have yet to be formulated*; nor—most fortunately—is it necessary to await a complete explanation in fundamental terms before

¹ See especially his *Mechanistic Conception of Life* (1912).

² v. Buddenbrock (1915), Bierens de Haan (1921), Alverdes (1932), Russell (1938), and others.

we attempt to analyse the behaviour of living things. Loeb's great contribution was the application of the experimental method to the reactions of animals, thus retrieving their interpretation from the vagueness and sterility of conjectural anthropomorphism and subjecting them to objective analysis. It must be admitted at once that any attempt to explain animal behaviour in terms of our present knowledge by one single embracing theory is premature; and while more can be learned by studying reactions to stimuli and classifying the responses of animals on a mechanistic rather than on a teleological basis,¹ and although higher functions can never wisely be called upon to explain an action if lower functions can provide a rational and consistent interpretation, there are many aspects of the behaviour of animals wherein a mechanomorphic scheme based solely on forced and stereotyped responses fails to meet the case and wherein the conceptions of motivation, incentive and learning can be more usefully and economically invoked.²

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¹ The value of the objective approach in comparison with the teleological as a stimulus to progress is seen in comparing two textbooks published about the same time—Warner's Jennings and Warner's *Introduction to Comparative Psychology* (N.Y., 1934) and the anthropomorphic *The Animal Mind: a Textbook of Comparative Psychology* by Sherrington (N.Y., 1936).

² See further p. 107.

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The Types of Motorial Responses

The behavioural responses of organisms to light are diverse and for three-quarters of a century workers in this field have made numerous attempts to rationalize them into a single system of classification. While terminology itself cannot claim to be an end of science—and, indeed, its apparent definiteness is often misleading—the labelling and classification of phenomena are of great value in the economy and clarification of thinking. Adequate classification, however, entails fundamental knowledge and it is not surprising in a subject which is still highly controversial and inadequately understood that agreement has not yet been reached.

In this connection several terms have been introduced into the literature. Strasburger (1878) in his revolutionary work on botany, wherein he made a fundamental study of the movements of plants, used the term PHOTOTROPISM ($\phi\omega\varsigma$, $\phi\omega\tau\acute{o}\varsigma$, light : $\tau\rho\omicron\pi\eta$, a turning) to describe the movements of sedentary plants in contradistinction to PHOTOTAXIS ($\tau\acute{\alpha}\xi\iota\varsigma$, a precise arrangement) to describe the locomotor reactions of freely moving organisms to light. Shortly thereafter, Engelmann (1883) introduced the term KINESIS ($\kappa\acute{\iota}\nu\eta\sigma\iota\varsigma$, a movement) to indicate reactions wherein the velocity of movement depended on the strength of the stimulus. The next contribution to terminology was due to Pfeffer (1904) who introduced the useful differentiation of PHOBOTAXIS ($\phi\acute{o}\beta\omicron\varsigma$, fear) to describe random, trial-and-error avoiding movements, and TOPOTAXIS ($\tau\acute{o}\pi\omicron\varsigma$, a place) to indicate directional attraction movements, while Kühn (1919-32) subdivided the latter into four categories of increasing complexity in response, which we shall adopt—TROPOTAXIS, TELOTAXIS, MENOTAXIS, and MNEMOTAXIS.¹ To these, Gunn and his colleagues (1937) added the term KLINOKINESIS and KLINOTAXIS ($\kappa\lambda\acute{\iota}\nu\omega$, bend) to express changes in orientation determined by turning movements. The term SCOTOTAXIS ($\sigma\kappa\acute{o}\tau\omicron\varsigma$, dark) suggested by Alverdes (1930) and Dietrich (1931) is probably unnecessary since those movements which may be interpreted as the result of an attraction to darkness are probably best looked upon as a negative phototaxis.

It is true that against this urge for classification some have rebelled (Mast, 1938), but although the dangers of a system of classification in concealing ignorance are obvious, its advantages are so considerable that as a tentative measure we will base our terminology on the classical scheme of Kühn, introducing some modifications advanced by Fraenkel and Gunn (1940). It is to be remembered, however, that the types of response are by no means mutually exclusive and that in their activities many animals show a combination of reactions.

A somewhat revolutionary view has recently been advanced by Viaud (1948). He divided the reactions of animals to light into two types :

¹ p. 43.

(a) "*Dermatoptic sensitivity*", a "primary" reaction of protoplasm to light evident throughout the cell in Protozoa and particularly in the surface layer in Metazoa ; and (b) "*visual sensitivity*", a characteristic of specific photoreceptor organs.

The first type of reaction is concerned with simple attraction towards (or repulsion from) light ; the second is concerned with orientation. The first has two distinct and reciprocal phases : the essential reaction is attraction towards the light (phototropism), purposeful in nature, elicited most readily by short-waved light, the response varying as the logarithm of the intensity of the stimulus (the Weber-Fechner law). Repulsion from light (photophobia), on the other hand, is a negative reaction, a phase of adaptation and recuperation in which the animal flees from light at its own particular speed. Visual sensitivity, on the other hand, is confined to the eyes and, concerning itself solely with visual orientation, responds most readily to stimulation by the mid-region of the spectrum. The first type of reaction is prepotent in lowly forms (such as *Hydra*) but becomes masked in higher forms by the second, although it again determines the animal's conduct when it is blinded (Crustaceans such as *Daphnia*, Rotifers such as *Asplanchna*) ; it cannot be elicited in forms higher than Amphibians. The second type of reaction does not appear in the lowest forms and in the higher adds visual apperception to its original function of spatial orientation. This is an interesting although somewhat speculative philosophy, and although all the complex story of orientation to light cannot be fitted into it as it stands, it may perhaps contain much truth.

In the scheme to be adopted here, the motorial responses of organisms to light will be divided into two main classes :

(a) PHOTOKINESES, *non-directional changes in random movements*. This implies merely a change of activity depending on the intensity of the stimulation, not on its direction ; for its initiation a mechanism is required sensitive only to changes in intensity ; there is no true orientation and the direction of the response is merely a matter of weighted chance.

(b) DIRECTIONAL ORIENTATIONS towards (*positive*) or away from (*negative*) the stimulating light. The term PHOTOTROPISM will be retained to indicate the directional orientation of parts of *sessile* plants and animals ; while the translatory movements of *motile* organisms will be described as PHOTOTAXES. It is obvious that these directional responses are more efficient and purposive than the more primitive changes in random activity, since they allow the organism to adapt itself more rapidly to the most favourable location in its environment.

To retain a sense of proportion it is well to remember that forms of stimulation other than light are operative on living organisms, although none shows the same interest and complexities in the responses elicited. The scientific conception of GEOTROPISM in plants to describe the effects of gravitational influences was introduced by Knight (1806) at a very early date, even before de Candolle (1832) formulated his theory of phototropism. Towards the end of the 19th century however, the study of the responses of organisms to various stimuli rapidly widened. In equally fundamental researches on the action of chemicals on the sperm of ferns and mosses, Pfeffer (1883-88) introduced the term CHEMOTAXIS. Stahl (1884) described HYDROTROPISM in fungi, Wortmann (1883) discovered THERMOTROPISM, and Verworn (1889) THIGMOTROPISM (contact stimulation; *θίγμυς*, touch) and GALVANOTROPISM. These, however, are not our present concern, and we shall proceed to exemplify shortly the various types of response to light.

It is also to be remembered that these various responses may be mutually additive; thus some flatworms are photo-negative and at the same time swim towards a cathode. When the two stimuli are presented together the response depends upon the direction and strength of each. Thus when the light and the cathode are at right angles the worm will swim at an angle bisecting the direction of the stimuli when the density of the current is proportional to the logarithm of the intensity of the illumination.

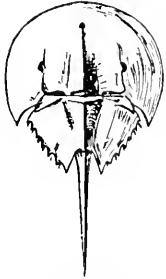
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PHOTOKINESIS

KINESSES (*κίνησις*, movement) are the most simple responses of motile organisms to light—they are merely *the alteration*, either a quickening or a slowing, of *normal random movements without specific directional orientation*; all that is required for their initiation is a mechanism of the simplest type which possesses the ability to react photochemically to variations in the intensity of illumination; specific photoreceptors (eyes) are in no sense necessary. The phenomenon is essentially the same in character as the alterations in metabolic activity produced by light which we have lately considered. It must be remembered, however, that a motorial response of this type but frequently more dramatic in nature may result from other stimuli such as variations in temperature or moisture.

The response may involve a change of velocity (ORTHOKINESIS) ($\acute{o}\rho\theta\acute{o}\varsigma$, straight) or a change in direction (KLINOKINESIS) ($\kappa\lambda\acute{\iota}\nu\omega$, turn).

ORTHOKINESIS, wherein *random movements are accelerated or decelerated according to changes in the intensity of the illumination*, is seldom the sole mode of response of any organism to light but usually reinforces reactions of another type. In its most dramatic form the organisms move while the stimulus acts, that is, so long as an intensity gradient exists; when the intensity becomes constant they come to rest. Viewed superficially this elementary response gives a false impression of orientation. Thus if the locomotor activity of an organism is increased by light and diminished in darkness, it aggregates preferentially in the shadowed region even if its movements continue to be random, just as the density of vehicular traffic increases as it is slowed in towns and decreases when speed is regained on the trunk roads; an organism with this reaction of a *high kinesis* in the light thus appears to show a negative phototaxis but can be said to be negatively phototactic with as much logic as the average motorist may be assumed to delight in traffic-jams.



King-crab



Whip-tail scorpion



Lamprey



Cockroach

This response of activity in a light-gradient and rest in the shade giving rise to an apparently photophobic tendency to aggregation in the dark is relatively common; it is seen typically in the *Bacterium photometricum* which, as its name implies, becomes active only under the influence of light, in many flat-worms,¹ in the maggot larvæ of various flies,² in certain Arthropods such as the king-crab³ or the whip-tail scorpion,⁴ in primitive Vertebrates such as the lamprey⁵ and in the larvæ of certain fish such as the herring, *Clupea*, and planktonic animals as a means of depth-control.⁶ The converse reaction is less common but is well exemplified by the inactivity of the cockroach in daylight and its activity in darkness.⁷

In higher forms these simple kinetic responses are less evident but stimulation of the eyes by light frequently has a dramatic effect on general activity. This is especially seen in Insects: thus in the cockroach, *Periplaneta*, exposure to light considerably reduces the threshold of response to other stimuli (Brecher, 1929), and as the intensity of light is increased the beetle, *Popillia*, walks more quickly (Moore and Cole, 1921).

KLINOKINESIS is of much wider application and interest; in it a change of direction is involved, so that *turning movements, normally*

¹ *Planaria*—Pearl (1903), Walter (1907); *Leptoplana*—Hovey (1929); *Plagiosomum*—Welsh (1933).

² Mast (1911), Herms (1911).

³ *Limulus*—Cole (1923).

⁴ *Mastigoproctus giganteus*—Patten (1917).

⁵ *Clupea*—Young (1935).

⁶ Woodhead and Woodhead (1955).

⁷ *Periplaneta orientalis*—Szymanski (1914), Wille (1920).

haphazard, are influenced by the intensity of light so that avoiding reactions occur by trial-and-error with the result that a devious path is taken in a general direction away from the light ; in a favourable environment the animal pursues a straight course, but entering an unfavourable environment it turns away. This may be accomplished by creeping or oscillatory movements as in Algæ such as diatoms and desmids (Pfeffer, 1904), by amœboid movements as in slime-fungi (Stahl, 1884) or the amœba (Mast, 1911), or by free-swimming movements by cilia as in the swarm spores of Algæ and some Ciliates (Oltmanns, 1922). In some Ciliates, for example, the direction of movement in a uniform environment changes periodically for no apparent reason so that the animal does not travel long in a straight line ; when exposed to illumination the rate of change of direction is

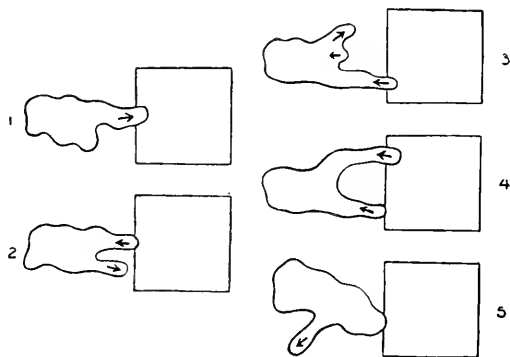


FIG. 13.—NEGATIVE KLINOKINESIS IN *AMŒBA*.

The organism is moving onto an illuminated cover-glass and eventually its movement is reversed (after Mast).

increased although the speed remains constant, so that they appear to avoid the light and tend to aggregate in shadow (Ulliyott, 1936). In comparison with orthokinesis whereby aggregation is reached entirely by chance, klinokinesis, although still haphazard, is obviously a more effective mechanism of orientation to attain an optimum environment either towards or away from the area of the highest concentration of the stimulus.

The simplest and most primitive response of this type is seen in the photo-negative kinesis of *Amœba proteus*, the reactions of which have received much study.¹ The reaction is extremely elementary. In a uniform environment this Rhizopod periodically throws out pseudopodia in an indiscriminate way and thereby effects movement. If, however, it is placed on a microscope slide with an illuminated

¹ Engelmann (1879), Davenport (1897), Mast (1910-32), Mast and Pusch (1924), Folger (1925-27), Luce (1926), Bovie (1926), Mast and Hulpieu (1930), and others.

square, a pseudopod on entering the square will stop for a moment, then protoplasmic flow will commence in the reverse direction, the pseudopod being finally withdrawn from the area. After repeated experiences of trial-and-error, pseudopodia appear on the opposite side of the animal and its whole movement is reversed (Fig. 13).

Before the response occurs there is a latent period which varies with the intensity of the light¹; and if the stimulus be intensified by the use of ultra-violet light, a single stimulus may be sufficient to reverse the direction of locomotion at once. It is also interesting that modifications in behaviour due to experience occur even in organisms so lowly as the amœba, for the time-reactions of the response are accelerated as the number of consecutive tests is increased, so that the animal becomes *habituated* to the stimulus (Mast and Pusch, 1924; Grindley, 1937).



Amœba

As would be expected in this lowly organism, the receptor mechanism is undifferentiated and the response is primitive; measurements of the elasticity of the plasmagel indicate that the change of movement is due to the gelling effect of radiation on the relatively fluid protoplasm² so that flow and the formation of pseudopodia are inhibited on the more highly illuminated parts but can occur readily in those parts of the organism on which the illumination is dim (Mast, 1932). The intimate nature of the mechanism whereby these changes are brought about is not known. It is noteworthy, however, that similar changes follow mechanical stimulation, and Folger (1926-27) concluded that since light and mechanical agitation produce the same changes and since the two are additive in the sense that the one stimulus can reinforce the other when both are subliminal, the response to the former is perhaps not specifically photochemical but of an even more primitive nature. It is also to be remembered that in some cases minute thermal increments are more effective than illumination, so that responses superficially accepted as photokinetic may in fact result from differential heating (differences as small as 0.0005° C are effective in the slime-mould, *Dictyostelium discoideum*, Bonner *et al.*, 1950).



Paramœcium



Dendrocoelum
(ciliated on
ventral surface)

More mobile Protozoa appear to react with greater effect. Thus ciliated species such as *Paramœcium* swim about haphazardly but if they approach a noxious stimulus (light, heat, acids, etc.) they back and turn and start off in a different direction, a process which is repeated until, leaving the stimulus behind, they can swim freely forward.³ A reaction which appears more complex is exemplified by the turbellarian flat-worm, *Dendrocoelum* (Ulliyott, 1936) (Fig. 14). This ciliated flat-worm never travels far in a straight line even if its environment is uniform, but if the intensity of light is increased, although its velocity remains unaltered, the changes in direction occur more frequently, a

¹ *Pelomyxa*—Wilber and Franklin (1947).

² That the amœboid movements of pseudopodia were due essentially to a gel-sol transformation in which the propulsive force is derived from the contractility of the elastic plasmagel was suggested by Wallich in 1863 and the theory was confirmed by Hyman (1917), Pantin (1924-26) and Mast (1926-31).

³ Ehrenberg (1838), Jennings (1906), Mast (1911), Rose (1929), and others.

response which decays with time as the organism becomes adapted. It follows that if travel in a certain direction exposes it to an increase in the intensity of light, the direction is changed by an increase in the rate of automatic turning and the worm eventually arrives in a

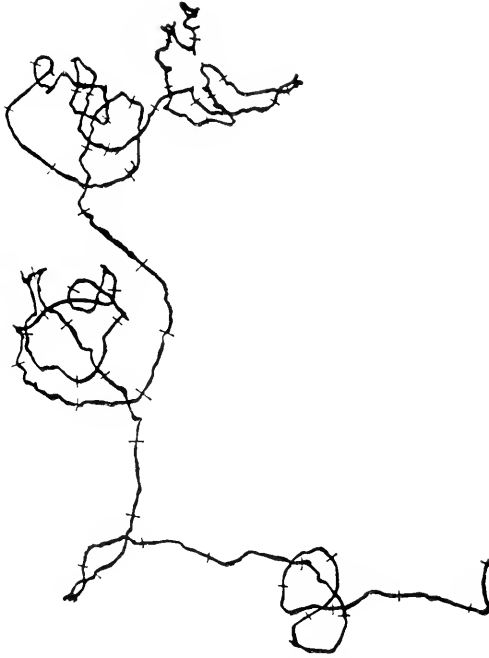


FIG. 14.—KLINOKINESIS IN A MOTILE ORGANISM.

Track of *Dendrocolum*. At the upper part of the figure illumination was turned on; turning movements are rapid. As their frequency decreases the path of the organism tends to straighten out so that it moves to an area of shadow. The velocity remains constant all the time; the cross-lines mark half-minute intervals (after Ulfvott, 1936).

haphazard way at the darker end of a gradient where a crowd tends to aggregate; moreover, if it crosses from a dark region into an area of bright illumination, an immediate increase in the rapidity of turning renders it very probable that its re-entry into the dark is speedy. It is interesting and significant that the reactions of this organism seem to have a sensitivity to light resembling that of the human eye (Pirenne and Marriott, 1955).

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PHOTOTROPISM

Used in Strasburger's (1878) original sense, the term PHOTO-TROPISM connotes *the orientation of sessile organisms towards or away from light*. The phenomenon is a widespread and well-known characteristic of plant life and as a rule the stimulus is the sun (HELIOTROPISM ;

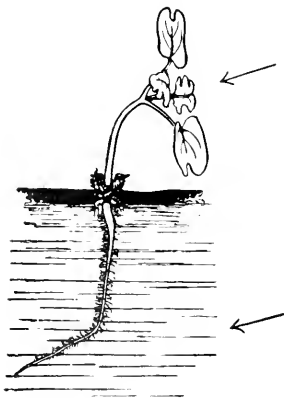


FIG. 15.—HELIOTROPISM.

Seedling of *Sinapsis alba* in water supported on a cork plate. It has been illuminated initially from all sides and then from one side only: the stem turns towards the light, the root away from it, and the leaf-blades at right angles to it (after Strasburger).

ἥλιος, the sun). Among the higher plants which are fixed in their habitat, heliotropic movements are limited to the component parts; the aerial vegetative axes usually turn towards the light, thus exhibiting a POSITIVE HELIOTROPISM, the leaf-blades take up a position at right-angles to the rays of light in order to receive as much illumination as possible (TRANSVERSE or DIA-HELIOTROPISM), while tendrils and roots grow from the light (NEGATIVE HELIOTROPISM) (Fig. 15). Occasionally these movements are remarkably delicate and rapid; thus the Bengal plant, *Hedysarum girans*, nods to a passing cloud. Sometimes, however, the axes of the plant are photo-negative; thus several grasses, corn and rice grow erect in darkness and tend to lie prostrate in bright illumination, becoming positively phototropic when shaded (Langham, 1941).

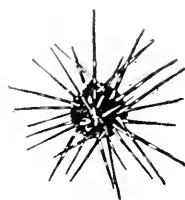
It is interesting that comparable non-translatory movements of the organs of animals may occur ; thus the hydroid, *Eudendrium*, and the marine polychæte worm, *Spirographis spallanzani*, show heliotropic bending movements (Loeb, 1890), some shell-fish open and others close their valves, clams retract their siphons (Hecht, 1919-20 ; Light, 1930), snails their tentacles (Grindley, 1937 ; and others) and sea-urchins, such as *Diadema antillarum*, move their spines if a light is flashed on them (P. and F. Sarasin, 1887 ; v. Uexküll, 1897 ; Millott, 1950), while many sedentary tubicolous polychæte worms, such as *Branchiomma*, withdraw into their tubes on a decrease in light intensity (Nicol, 1950).

An interesting variant of this reaction is seen in certain sea-urchins such as the European *Strongylocentrotus* (Dubois, 1913) and the Caribbean *Lytechinus* (Millott, 1957), which normally withdraw their podia when illuminated. When lying in sunlit waters these echinoids gather small stones, the shells of bivalve molluscs, pieces of seaweed or whatever debris may be within reach of their tube-feet, and heap them upon themselves, using them as a parasol to protect themselves from light.

The mechanism of the phototropic responses of plants is now relatively clear. They are due to the production of growth-regulating phytohormones¹ called AUXINS, a generic term applied to a number of related chemical substances of wide distribution formed by specialized parts of the plant—the tip of the coleoptile in seedlings and the leaves, particularly the young leaves, of mature plants. There these hormones are formed from precursors on stimulation by light and thence they are transported throughout the tissues of the plant at a rate more rapid than can be accounted for by simple diffusion (about 10 mm. per hour) ; as it travels through the tissues the freely-moving auxin regulates the varying rates of growth that account for such phenomena as photo- and geotropism, while some of it becomes bound in the tissues, there to regulate normal growth. In phototropic curvature the freely available hormone becomes unequally distributed in its passage along the two sides of a laterally illuminated plant, an increase of concentration on the shaded side of the stem leading to a bending of the organ. Its precise mode of action is unknown, but it would seem probable that, in addition to other activities such as the regulation of osmosis, it acts essentially as a co-enzyme in the respiratory activity of the cells, causing them to elongate and sometimes stimulating them to divide.

In these processes determining the phototropic movements of plants—and also of animals—carotenoid pigments act as sensitizers. These pigments are quite different in chemical structure and absorptive properties from the chlorophyll group of pigments which are primarily responsible for the photosynthesis concerned with metabolism in the vegetable kingdom² ; they will be more fully described at a later stage³.

We have already seen that de Candolle (1832) first, and Sachs (1882-87) at a later date showed that light was responsible for the directional growth of



Diadema antillarum



Branchiomma

¹ p. 547.

² p. 5.

³ p. 118.

plants, and since most plants bend towards the light, it was generally assumed that it had a retarding influence upon growth, a view elaborated in great detail by Blaauw (1909-18). That an explanation so simple could not account for the facts, however, had already been shown in the classical researches of Darwin (1880) on the behaviour of seedlings of grass (*Phalaris canariensis*) and the oat (*Avena sativa*)—observations from which all modern views on the mechanism of phototropism have directly descended. Darwin showed that the seedlings only curved towards the light when the tip of the coleoptile was unilaterally

FIGS. 16-20.—PHOTOTROPISM IN SEEDLINGS.

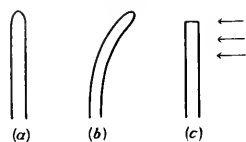


FIG. 16.

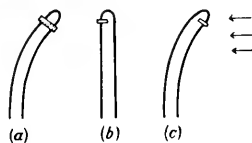


FIG. 17.

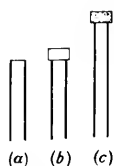


FIG. 18.

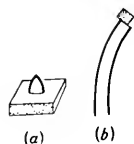


FIG. 19.



FIG. 20.

FIG. 16.—Darwin, 1880. The grass coleoptile exposed to lateral illumination (a) bends towards the light (b). When the tip is removed (c) the phototropic response does not occur.

FIG. 17.—Boysen-Jensen, 1910-11. When a coleoptile tip is excised and replaced with gelatin inserted between it and the stump (a), phototropic curvature results normally; a diffusible substance therefore passes across the plate of gelatin. If, however, a plate of mica is inserted on the shaded side (b), no response occurs. If the mica is inserted on the illuminated side, the response is normal (c). It follows that the diffusible substance passes down the shaded side.

FIGS. 18-20. Went, 1928.

FIG. 18. When the tip of the coleoptile is removed, growth in length ceases (a). An agar block placed on the stump has no effect (b). An agar block containing juice extracted from the excised tip promotes normal growth (c).

FIG. 19. The coleoptile tip is placed upon an agar block (a), and a piece of the block transferred unilaterally to a decapitated coleoptile (b). Unilateral growth resembling phototropic curvature results due to the diffusion of the hormone from the agar derived from the tip.

FIG. 20.—When unilateral light falls on an excised tip in contact with two agar blocks separated by a razor blade, the greater part (65%) of the growth-hormone is recovered from the agar on the shaded side.

illuminated and never when it was shaded by tinfoil even while the rest of the plant was exposed, and that no curvature ever occurred in the stem or the root if the growing tip were removed (Fig. 16). This localization of sensitivity to the growing tip of the seedling was confirmed by subsequent workers. Rothert (1892-96) incised the vascular bundles in various places and proved that the phototropic stimulus travelled from the sensitive tip throughout the plant in the parenchyma, while Fitting (1905-7) observed that the curvature was caused by a difference in the rate of growth of the two sides, in positive phototropism the darkened side growing more rapidly than the illuminated side. The next

fundamental step was due to Boysen-Jensen (1910-13) who showed that the stimulus could traverse a layer of gelatine but was arrested by a plate of mica, thus demonstrating that the curvature was due to the diffusion down the shaded side of the plant of a chemical substance stimulating growth (Fig. 17). These observations were confirmed by Paál (1914-18) who showed, moreover, that if an unstimulated tip were excised and replaced towards one side of the stump, growth was accelerated on that side, thus demonstrating that the stimulatory substance was continuously formed in the sensitive region. The final proof was effected by Stark (1921), Stark and Dreehsel (1922), Cholodny (1927-35) and especially by the Dutch botanist, Went (1926-45), who trapped the diffusible growth-hormone descending from the coleoptile tip in a piece of gelatine or agar inserted into the plant and, transferring the jelly from the plant and placing it on the cut end of a non-illuminated plant from which the tip had been removed, demonstrated the occurrence of a typical phototropic response in the second even although light had been entirely excluded (Figs. 18-20). All that remained was to identify the chemical nature of the active agent.

A growth-hormone of this type was first extracted from fungi by Nielsen (1930) and Boysen-Jensen (1931), and shortly thereafter was chemically identified by Kögl (1932) and Kögl and Kostermans (1934) as 3-indole-acetic acid. Subsequent intensive research, particularly by Kögl and his colleagues (1931-35) in Germany, Zimmerman and Hitchcock and their colleagues (1935-48) in the Boyce Thompson Institute for Plant Research in New York, has shown that there are many such physiologically active substances (*auxins*) of wide distribution; indeed, over 50 compounds, natural and synthetic, having this growth-producing property had been isolated by 1935. The most interesting historically are *auxin a* (a monocyclic trihydroxy-carboxylic acid, $C_{18}H_{32}O_5$), *auxin b* (a monocyclic hydroxy-keto-carboxylic acid, $C_{18}H_{30}O$), and *heterauxin* (3-indole-acetic acid, $C_{10}H_9O_2N$) (Kögl, 1935). Whether the first two or other allied substances are present in the living plant is not clear; but the most popular hypothesis at present is that heterauxin is present in the tip of the stem initially as a precursor: here it is activated into freely moving auxin by enzymic action; and it would appear that its activity may be masked or reduced by anti-auxins. However that may be, it is clear that such substances applied to the intact plant or inserted into incisions or fed to the plant through the soil not only induce tropic curvatures but can modify the plant in size, shape, pattern and texture, can inhibit the formation of buds and perhaps of flowers,¹ and in supra-physiological concentrations can induce tumour-like growths.² It is puzzling why the same substances are found in human saliva (Seubert, 1925) and urine (Kögl and Smit, 1931).

It is interesting that an artificial end-organ to stimulate phototropic activity can be synthesized (Brauner, 1952). If capillary tubes filled with photosensitized indolylacetic acid are substituted for the cotyledons in *Helianthus* seedlings, illumination of one produces a marked curvature of the other hypocotyl.

This description may give the impression of over-simplification. It must not be thought that the whole story of the growth of plants is explained in terms of a single auxin. Research in progress as this book is being written is showing that the regulation of growth is based on a complex system of several auxins, kintin-like hormones and gibberellin-like hormones, and possibly other related substances.

¹ p. 12.

² For general reviews, see Boysen-Jensen (1936),¹ Went (1939), Zimmerman (1948), van Overbeek (1956), Bentley (1957).

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PHOTOTAXIS

A DIRECTED RESPONSE TO LIGHT is obviously a much more efficient orientating mechanism than the simple change in activity we have already discussed as photokinesis wherein a difference of intensity serves as the stimulus and aggregation is determined, as it were, merely by accident. The phototactic reaction is *purposive*; for example, by suitable manipulation of the lighting system it is possible to make

certain photo-positive animals travel towards a light even although this movement brings them into a region of lower intensity of illumination,¹ or certain photo-negative animals to seek a dark shelter even although this entails moving towards a light.² It is a response, however, which requires one or more receptor organs specially designed to appreciate the direction of the incident light rather than merely changes in its intensity, and as the response becomes more and more efficient and therefore more and more complex, the receptor organs become progressively specialized until they eventually achieve the structural differentiation necessary to mediate the faculty of vision. The directional phototropic movements of sessile plants are slow and leisurely, essentially kinetic in nature, quantitative in type and chemical in execution ; but motile organisms require a more efficient mechanism capable of qualitative responses—a shock-reaction eventually mediated by nervous activity. The difference between the two types of response is well exemplified in the mutilation experiments of Viaud and Médioni (1949) on the flat-worm, *Planaria lugubris*, an animal in which both reactions are present ; they found that its positive photokinesis was entirely due to the action of light on the skin while positional orientation by phototaxis depended on the eyes.

As they evolved, these phototactic responses increased in complexity and efficiency ; the various stages may be classified as follows (Kühn, 1919–32 ; Gunn *et al.* 1937).

(i) KLINOTAXIS (κλίνω, turn ; τάξις, a precise arrangement), wherein turning movements, normally alternating regularly, are directed towards or away from the light. One receptor organ only is necessary which responds by comparing the intensities of *successive* stimuli as the organism turns, and the directional path is consequently irregular and wavy.

(ii) TROPOTAXIS (τροπή, a turn), wherein orientation is effected by the *simultaneous* comparison of the intensities of the stimulation of two symmetrical receptors and the maintenance of a bilateral balance. The path is thus continuously corrected so that it is practically straight towards or away from the light, and it is obvious that greater accuracy and precision are obtained by a simultaneous comparison than by comparing present experiences with past.

(iii) TELOTAXIS (τέλος, a goal), a direct orientation towards or away from the light without the necessity of bilateral balance. A single receptor organ which can fixate the source of light is sufficient for its initiation, but it must possess a number of elements spatially distributed so that the stimulus can be localized on the sensory surface and the head and body can be orientated directly in line with the light.

¹ See the experiments of Richard (1948) on termite larvæ (*Calotermes flavicollis*).

² See Goustard (1948–50) experimenting on the cockroach, *Blattella* ; Bolwig (1954) experimenting on the stomatopod, *Gonodactylus*.

(iv) MENOTAXIS (*μένειν*, to remain). Orientation is not directly towards or away from the light but at an angle to it ; the animal appreciates a definite distribution of the stimulus over its retina where it retains the impression, and having evolved beyond the ability to travel only in a straight line, it can orientate itself and accomplish separate reactions with reference to different parts of its field of vision. This activity is exemplified in the light-compass reactions of insects, or the dorsal (or ventral) light reaction of fishes.

(v) Kühn's final category, MNEMOTAXIS (*μνήμη*, memory), wherein immediate orientation is aided by memory-images of past experience, is associated with other methods as an adjuvant mechanism of a higher type.

In these responses to light three stages emerge in the evolutionary process. In the simplest and most primitive response, the stimulus is appreciated in an indeterminate manner and orientating movements are corrective. In the next stage a more complicated but obviously more efficient reflex mechanism ensures a directed and purposeful orientation. The third and highest development involves the ability to retain the impression made upon the receptor organ, to adjust the response and utilize various means to gain the desired end should the most obvious fail ; it is a purposive rather than a reflex response. This more advanced development is exemplified in its simplest terms in the continued ability of some worms to orientate themselves to light when one eye has been removed, or in the compensatory modifications in the responses of certain insects when some of the legs on one side have been removed ; the same adaptability is seen in the complicated manoeuvres of ants, backwards, sideways or forwards, to reach the desired goal, and reaches its highest forms in the reactions of Vertebrates among which its culmination is seen in the navigational ability of birds.



Drosophila

All these reactions, however, whether simple or complex, have certain features in common. In the first place, *they are all innate and show no evidence of being acquired* ; thus Payne (1910-11) bred the fruit-fly, *Drosophila*, in the dark and found that individuals of the 69th generation were normally photo-positive at the first trial ; while the young bird may set out on its first migration to a new land 2,000 miles away and follow by a light-compass reaction approximately the same route as its parents. It is true that the standard responses may become altered by use, being either accentuated by habituation (as we have seen even in *Amœba*, Mast and Pusch, 1924),¹ or diminished by adaptation (as we shall see in some insects, Clark, 1928-33) ; but these are physical processes. It is also true that their efficiency may be increased with training, as is seen in the migration or homing of birds (Ruppel and Schein, 1941 ; Matthews, 1953), or can be altered and even

¹ p. 36.

inhibited by associations established by conditioned reflexes ; thus the photo-negativity of the cockroach, *Blatella*, can be inhibited by training if a light is placed over its dark shelter (Goustand, 1948-50). It is also to be remembered that the removal of necessary effector organs may inhibit or invert a normal phototactic response even although these have no apparent connection with photoreceptors (the antennae of the cockroach or the wings of the fruit-fly, *Drosophila*, Goustand, 1949).

In the second place, *these responses are all of biological value* and to attain this end they may vary with the strength of the stimulus or change their character if associated with a second stimulus of another nature ; moreover, they may alter in type and even reverse their nature during the life of the animal to meet the needs of a change in environment.

Thus the usual photo-negative response (the *shadow-reflex*) seen in so many worms and molluscs is essentially an escape movement from the presence of predators, while the opposite response of the tentacle of the snail is the expression of the fact that a shadow usually signifies food. Some of these responses are very sensitive : thus the acorn-shell, *Balanus*, responds to a darkening of 5% (v. Buddenbrock, 1930). The simplest example of a variation in the response with the strength of stimulus is seen in the protozoon, *Euglena*, which is photo-positive in weak and negative in strong light so that it orientates itself to favourable mid-intensities (Mast, 1938), or in the fruit-fly, *Drosophila*, which is positively phototactic in illuminations below 9 lux and negatively over 79 lux (Médioni, 1954). A similar variation may occur with the nature of the light ; thus the flat-worm, *Planaria lugubris*, is said to be positively phototactic to red and negatively to blue light (Viaud, 1949). Again, other environmental circumstances may alter the response. *Paramecium* is geo-positive in the light and negative in the dark (Fox, 1925) ; the normal negative phototaxis of the goldfish, *Carassius auratus*, disappears if the temperature is increased by 10° C (Andrews, 1952) ; the normal positive phototaxis of the tsetse-fly, *Glossina*, becomes negative if the temperature is raised above 40° C even if the temperature in the dark is so high that it drops down dead (Jack and Williams, 1937) ; exposure to dry air alters the phototactic reaction of the woodlouse, *Armadillidium*, from negative to positive (Henke, 1930) ; while the negative response of the oligochaete, *Perichæta*, when it is extended can be changed to a positive response when the worm is contracted (Harper, 1905).

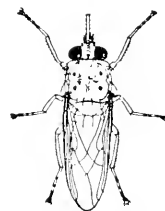
An excellent example of a change in response with different combinations of stimuli is seen in the behaviour of *Littorina neritoides*, a tiny mollusc which inhabits the rocky shores of European seas. Fraenkel (1927) showed experimentally that it was always geo-negative, photo-negative always when out of the water and when normally orientated in the water, but photo-positive when



Balanus



Carassius



Glossina



Littorina



Forficula

Two members of
Polyzoan colony

Caterpillar



Anguilla

in water and upside-down, one stimulus (the presence of water) thus modifying the influence of another (light). Its geo-negativity drives it to the surface of the sea and if it surfaces in bright light it returns to the water because of its photo-negativity ; if it surfaces beneath a submerged rock its positive phototaxis makes it crawl beneath it in the upside-down position until, reaching the air, its negative phototaxis keeps it in a shaded cleft. Again, when the gardener traps an earwig in a flower-pot containing dry straw inverted on a cane, he is utilizing the fact that *Forficula* demonstrates photokinesis, thigmotaxis, hydrokinesis and negative geotaxis.

A change in response during the development of the animal is well exemplified in the case of some marine worms ; these are usually photo-positive when they leave the egg so that they come to the surface and swim ; at a later stage they become photo-negative with the result that they burrow in the mud and crawl (Mast, 1911). The larvæ of the polyzoan sea-mat, *Bugula*, similarly disperse under a positive phototaxis, but after a few hours turn photo-negative so that they attach themselves to the bottom and undergo metamorphosis (Grave, 1930 ; Lynch, 1949).

These changes may be associated with stages in the development of the visual cells. Thus the larvæ of the cat-fish, *Ameiurus*, are initially unresponsive to light at a stage when the visual elements are not fully differentiated ; later they become photo-negative, a phase during which the rods and cones are contracted and show no retinomotor reactions ; finally the larvæ become photo-positive, a phase characterized by the commencement of retinomotor reactions (Armstrong, 1949).

A change in response may also accompany a change of habit. Thus young caterpillars of *Porthesia* are strongly photo-positive when they are hungry, a response which normally leads them upwards to the leaves of their food plant, but the response is lost after feeding ; while male and female ants become temporarily photo-positive at the time of their nuptial flight, a reaction lost when they shed their wings (Loeb, 1918).

Another interesting example of this type of change to suit a marked change in habit is the common eel, *Anguilla*. At the stage of sexual maturity in the autumn when it leaves fresh water to migrate downstream on its journey to its mating grounds in the Sargasso Sea, there is a great increase in the size of the eyes and the fish becomes photo-negative. This season coincides with the safety afforded by floods and moonless nights and the fish avoids the light to such purpose that its nuptial journey can be checked and the eels diverted into traps in large numbers by means of underwater lights shining upstream (Lowe, 1952).

A phototactic response of this type may be so prepotent that, although generally biologically useful, it may drive the animal to destruction. Thus the stimulus which leads the moth to fly towards the sun will drive it into the candle-flame ; the same response in the newly hatched larva of *Euproctis* which normally leads it upwards towards the leaves of its food plant will force it to

migrate downwards to starvation if illuminated from below (Loeb, 1918 ; Lammert, 1925 ; v. Buddenbrock, 1930) ; while, provided the stimulating light is sufficiently bright, the negative phototaxis of the larva of the bluebottle, *Calliphora*, will induce it to approach a source of ammonia of lethal concentration (Hurst, 1953).

- Andrews. *Physiol. Zool.*, **25**, 240 (1952).
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The Types of Phototactic Response

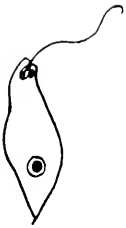
We shall now proceed to exemplify the various types of phototactic responses ; but, as we have just seen, it is to be remembered that animals usually orientate themselves in more than one way depending on the circumstances prevailing. It is less correct to say, for example, that an animal is telotactic than that it may exhibit a telotactic reaction. Thus, as we shall see, some ciliated Protozoa or worms show an undifferentiated photokinetic response with one stimulus and a klinotactic or tropotactic response with another, while in its complex but very efficient mechanism of orientation, the honey-bee combines tropotaxis, telotaxis and menotaxis with mnemotaxis.

KLINOTAXIS

The most primitive directed orientation to light is by KLINOTAXIS whereby *turning movements, normally alternating regularly, are specifically orientated* with respect to the light. This is well exemplified in the behaviour of flagellated or ciliated Protozoa or the maggot larvæ of certain common flies. Each of these shows a different type of response. The Protozoa orientate themselves as a result of successive stimuli falling on a photosensitive organ periodically exposed as they rotate

longitudinally by means of cilia, maggots by muscular contraction as they crawl.

The Flagellates, protozoans which swim by means of a flagellum much after the manner of a gondolier, in reverse, with his single oar, are frequently photosensitive. Some of them retain a primitive photokinetic response whereby they become inactive in low illumination and resume activity if the light is increased. This simple kinetic response determining general activity is, however, supplemented by a shock-reaction which determines orientation; for this purpose they have evolved a sensitized area specially modified for the reception of the stimulus. In a homogeneous environment they take a direct course undergoing continuous rotation on a longitudinal axis as they are propelled by the flagellum; to variations of the intensity of light they respond by abrupt changes in the rate and direction of movement either towards or away from the light. Once orientated they are not held on a direct course by the continuing action of light, but if they diverge, the orientating stimulus changes and immediately recalls them automatically. The automaticity of the response is seen if the field contains two beams of light crossing at an angle, in which case these organisms orientate themselves and proceed in a direction between the two beams determined by their relative intensities and angles of incidence (Buder, 1917; Mast and Johnson, 1932). Their photic responses have been studied most fully in the typical species, *Euglena*, a transparent green Protozoon photo-positive in weak, photo-negative in strong light.¹



Euglena

Euglena viridis, the flagellate infusorian which commonly forms the green scum on stagnant fresh water, has a photosensitive "eye-spot" or "stigma"² situated in the concavity of a pigmented shield³ in close association with the root of the flagellum; the arrangement is such that when the surface of the eye-spot is illuminated the photosensitive substance at the base of the flagellum is thrown into the shadow (Fig. 80). It follows that rotation of the transparent organism on its longitudinal axis produces an alternate shading and exposure of this substance unless it is orientated so as to proceed directly towards or away from a light (Fig. 21). If the direction of the rays is changed through 90° to illuminate the organism laterally, no reaction occurs until the rotation brings the eye-spot to face the light thus throwing the photosensitive area into the shade; thereupon the organism suddenly bends away from the light, and, continuing rotation thus, gradually straightens, a response which is repeated on each rotation so that it is soon proceeding again directly away from the new direction of the light. Subsequent rotation in this position no longer produces changes in the intensity falling upon the two surfaces and the organism therefore proceeds uninterruptedly in this direction.

¹ Verworn (1889), Jennings (1904), Mast (1911-38), Bancroft (1913), Buder (1917), Mast and Gover (1922), Mast and Johnson (1932), and others.

² p. 126.

³ The pigment is *astaxanthin*, p. 120.

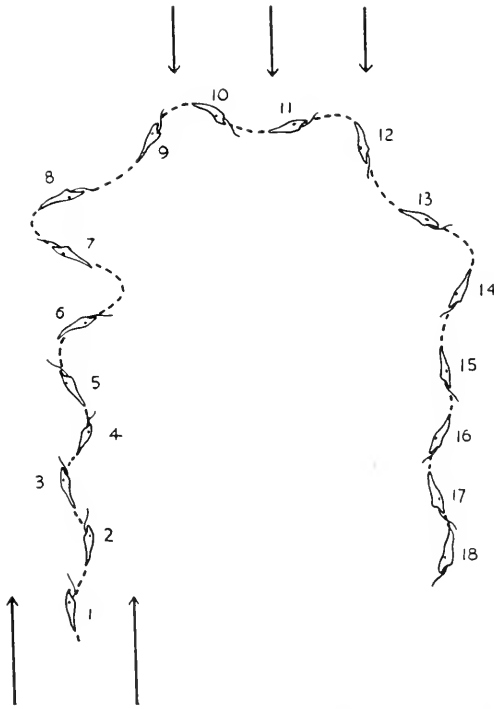


FIG. 21.—KLINOTAXIS IN A SWIMMING ORGANISM.

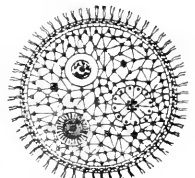
The orientation of *Euglena viridis*. The orientation of the organism as it swims away from the light (coming from below) rotating in a wavy path (1 to 6). At 6 the direction of the light is reversed to come from above; each time the receptor area is shielded by the pigment the organism swerves to the dorsal side. After an initial wavy course (7 to 8) it bends laterally across the path of the beam, and from 13 to 18 it again swims as before away from the light (after Jennings, 1906).

The Ciliates, which orientate themselves by means of cilia much as a rowing boat without a rudder, react phototactically in a similar manner (Fig. 22). Thus *Stentor coeruleus*, a trumpet-shaped¹ Protozoon, the bell of which is surrounded by cilia within which is an eccentrically placed mouth, exhibits the same reaction by virtue of the fact that the oral surface is more photosensitive than the aboral (Jennings, 1904; Mast, 1906-11).



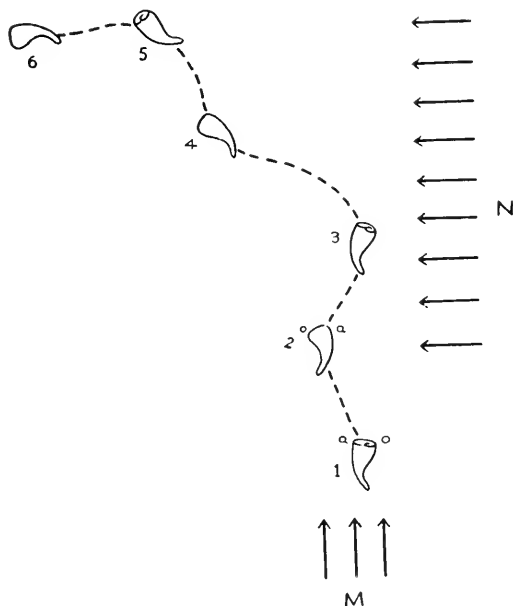
Stentor

A similar arrangement multiplied many-fold is seen in colonial forms, such as *Volvox globator*, a green organism found in fresh-water pools, formed of a hollow spherical colony of some 10,000 individual zooids each of which is equipped with two flagella and a stigma protected on one side by a pigmentary shield; stimulation of the sensitive area results in the translation of the diagonal



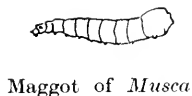
Volvox

¹ The name is from Stentor, the herald of the *Iliad* who had a loud trumpet-like voice.

FIG. 22.—KLINOTAXIS IN *STENIOR CERULEUS*.

In 1 and 2 the organism is seen swimming away from the light shining from behind it (indicated by the lower arrows, M). As it swims it rotates so that the oral side (*o*) and the aboral side (*a*) are equally stimulated. At 3 the original light is turned off and a lateral light (indicated by the side arrows, N) is turned on. As soon as the oral side faces the light the organism turns rapidly away to position 4 and continues in this sense until, at 6, the oral side is approximately equally exposed to light in all positions on the spiral course (after Mast, 1911).

stroke of the flagella into a backward sweep, the whole number beating in unison and thus orientating the colony in the required direction (Mast, 1906-27 ; Mast and Johnson, 1932).

Maggot of *Musca*Maggot of *Calliphora*

Crawling organisms such as the maggots of flies (the house-fly, *Musca domestica*, the bluebottle, *Calliphora erythrocephala*, etc.) were among the first organisms to be investigated in this way.¹ Their phototactic response is somewhat different from that of swimming Flagellates or Ciliates. Although the photosensitive structures are exceedingly primitive, the anterior end of the larva is negatively responsive to light. When crawling it raises its head in the air and alternately deviates to either side as if in exploratory movements ; on lateral illumination, the head is swung violently away from the light, a reaction which is repeated, turning the animal round until the head is equally illuminated at two successive deviations, whereupon it crawls directly

¹ Pouchet (1872), Holmes (1905), Loeb (1905-18), Mast (1911), Herms (1911), Patten (1914-16), Ellsworth (1933), Welsh (1937).

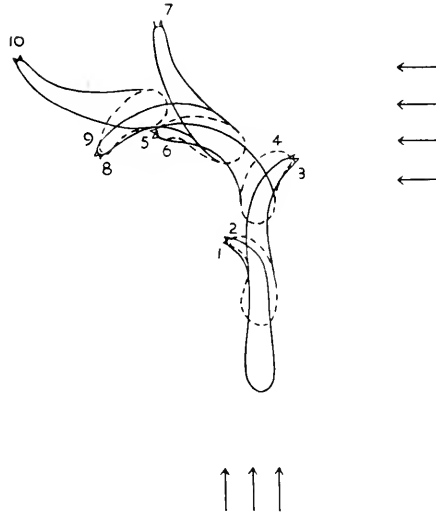


FIG. 23.—KLINOTAXIS IN A CRAWLING ORGANISM.

The maggot is photo-negative and crawls away from the light (below). From the initial position, 1, it contracts into 2, elongates into 3 and contracts again into 4, each time swinging its head across to one or other side. So long as the sides of the head are equally illuminated its path is straight. At 3, the lower light is switched off and the side light switched on; the organism immediately swings violently into position 5. Thereafter it contracts to 6, and, having swung in the opposite direction to 7, again receives preferential illumination on the side. It therefore swings again violently to 8 and, having contracted to 9, proceeds again, as before, directly away from the light (10) (after Mast, 1911).

away from the light (Fig. 23). If a light is persistently flashed on the same side on each deviation of the head, a circus movement is produced, and if two directed lights are simultaneously employed the animal crawls away at a direction half-way between the two beams if they are equal, or proportionately more nearly in line with the brighter beam if they are unequal (Patten, 1914).

- | | |
|---|---|
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N.Y. (1911). |
| Buder. <i>Jb. wiss. Bot.</i> , 58 , 105 (1917). | <i>Biol. Zbl.</i> , 34 , 641 (1914). |
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183, 225, 261, 312 (1872). |
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TROPOTAXIS

In tropotaxis at least two symmetrical receptor organs are necessary, and instead of relying on successive exposures of a single receptor

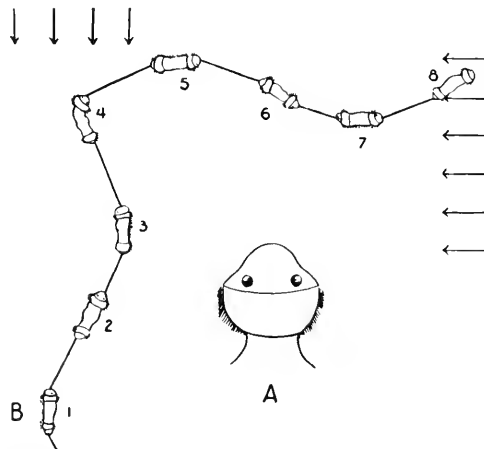


FIG. 24.—THE TROPIC RESPONSE OF LARVA OF *ARENICOLA*.

A. The head of the larva with two symmetrical eyes.

B. The path of movement of the larva: in 1 to 4 the light remains stationary; in 5 to 8 it is placed at right angles (after Mast).

by trial movements, *the animal orientates itself by the simultaneous comparison of the intensity of stimulation on the two sides*. In the simple forms inequality of stimulation leads to orientation in the required direction by a reciprocal coordination of the muscles of either side of the animal controlled by the nervous system: if there is an excess of stimulation on one side, a turning movement occurs; if equality, the stimuli cancel each other out and the animal progresses straight forwards; and if it subsequently strays from its path a renewed inequality corrects the deviation. It follows that if two sources of light appear simultaneously the animal orientates itself directly between them in proportion to their relative intensities.

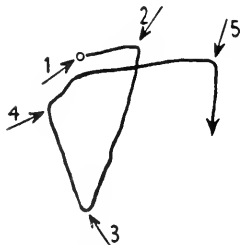


FIG. 25.—NEGATIVE TROPOTAXIS.

The path of the flour-moth larva, *Ephesia*, starting from the small circle with a light shown as indicated by the arrow, 1. Each successive number indicates the position of a new light turned on when the animal reached the corresponding point on its track; its direction changed in a straight line directly from the light (after Brandt).

The larvæ of some marine worms provide the most simple type of this reaction; they swim by the activity of cilia but orientation is the result of muscular contraction. Of these, the larvæ of the polychæte worm, *Arenicola*, have been most intensively studied (Mast, 1911; Garrey, 1918). These are minute creatures with two eyes anteriorly and a band of cilia at either end; as they swim they rotate longi-

tudinally so that on lateral illumination each eye is alternately illuminated and shaded. As each eye becomes exposed to the light, the muscles of the illuminated side contract violently turning the head towards the light (Fig. 24). Since this occurs twice during each rotation, the larva is rapidly orientated towards the light until the two eyes are equally illuminated all the time, whereupon further muscular contraction and orientation cease.

A very similar and typical reaction is seen in the rotifer, *Branchionus* (Viaud, 1948), and in the photo-negative larvæ of the flour-moth, *Ephesia*, which are provided on either side of the head with an aggregate eye composed of six ocelli (Brandt, 1934) (Fig. 25).

A further evolutionary step is seen in earthworms. As is the general rule, impulses originating in the photoreceptors on one side of the body determine orientation by inducing a simple reflex contraction of the muscles on the opposite side, but it is obvious that if these impulses can be modified and integrated in the central nervous system, a more effective response is obtained.

Such responses have been fully studied in the earthworm, *Lumbricus terrestris*, and *Eisenia fetida*.¹ In these animals the existence of photoreceptor organs associated with a subepidermal nerve-net was demonstrated by Richard Hesse (1896) and confirmed by W. N. Hess (1925)²; they are most numerous and receptive near the anterior extremity of the animal. The response to light is somewhat complicated and has given rise to some difference of opinion; but it would seem most likely that if the worm is sluggish and is exposed to dim light, it slowly extends, turns its anterior end away from the light, and continues to move thus. If, however, the worm is active when it is illuminated from the side, the anterior end is quickly raised and turned in the direction opposite to that in which it happens to be, whether it is directed to the light or not, and thereafter swung from side to side, a position and direction being eventually adopted in which the anterior end is least exposed to the light.

If now the cerebral ganglion is removed or destroyed or if it is inhibited by a reduction of temperature or the injection of depressant drugs such as cocaine or alcohol, the opposite reaction of a positive phototaxis results; in these circumstances lateral illumination of the more posterior photoreceptors produces a contraction of the muscles of the same side which causes the worm to turn towards the light, a reaction due to reflexes mediated through the ventral cord (Hess, 1924; Prosser, 1934). It would seem that normally this weak positive ipsilateral response mediated through the cord is overshadowed by the stronger negative contralateral response derived from the receptors in the highly sensitive anterior end and mediated by the cerebral ganglion, and that the final response of the animal is the resultant of the two antagonistic tendencies after integration and coordination in the central nervous system.

It is obvious that the bilateral balance of the tropotactic response will be upset if one eye is blinded, either by painting it over or by its removal, so that with lateral illumination the animal will tend con-

¹ Loeb (1894), R. Hesse (1896), Parker and Arkin (1901), Smith (1902), Adams (1903), Holmes (1905), Harper (1905), Mast (1911), W. N. Hess (1924), Nomura (1926-27), Prosser (1934), and others.

² pp. 131, 518.

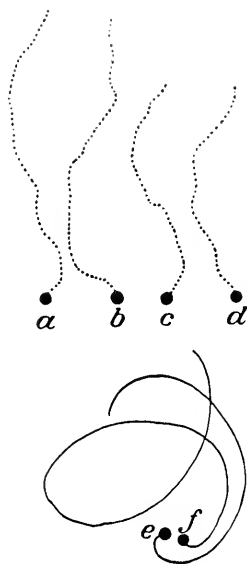


FIG. 26.—POSITIVE TROPOTAXIS.

The tracks taken by the woodlouse, *Armadillidium*, blinded on the right side. *a, b, c, d.* The tracks of the louse in darkness. *e, f.* Circus movements with the light overhead (after Henke).

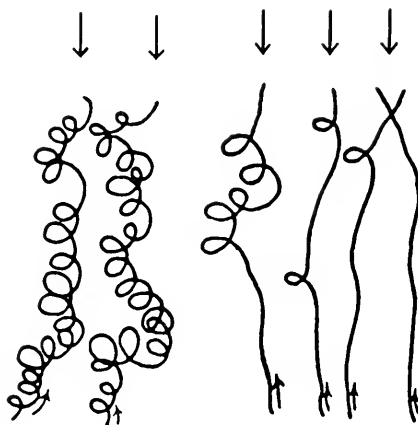


FIG. 27.—CIRCUS MOVEMENTS IN A UNILATERALLY BLINDED *NOTONECTA*.

The animal directs itself towards the light above, indicated by arrows. The illustration shows the path taken in repeated trials. From left to right, the tracks are the 1st, 3rd, 35th, 39th, 41st and 43rd attempts. It is seen that the initial attempts are circus movements which gradually straighten out until eventually, after some trials, the track is almost straight (after Clark, 1928).



Armadillidium

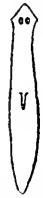
stantly to deviate towards one side, or in an overhead light to perform circus movements. This deviation towards the seeing side after unilateral blinding is well seen in the case of the woodlouse, *Armadillidium*, a Crustacean which lives under stones or decaying wood (Henke, 1930) (Fig. 26). In some instances these abnormal deviations occur for an indefinite time,¹ but in others a process of adaptation sets in so that the circus movements gradually cease and the path eventually straightens out² (Fig. 27). An exception to this type of behaviour is seen in the evolutionary development of the tropotactic response whereby each eye becomes regionally differentiated so that each can act as a symmetrical pair of organs. Thus the eyes of some worms and insects possess two functionally different regions one of which initiates

¹ The snail, *Helix*—von Buddenbrock (1919); the millipede, *Julus*—Müller (1924); the silverfish, *Lepisma*—Meyer (1932); the larva of the flour-moth, *Ephestia*—Brandt (1934).

² The water-boatman, *Notonecta*—Holmes (1905), Clark (1928), Lüdtke (1935–42); the robber-fly, *Proctacanthus*—Garrey (1918); the whirligig beetle, *Dineutus assimilis*—Clark (1931–33), Raymont (1939).

turning towards one side and the other in the opposite direction ; although the responses are typically tropotactic in nature, the telotactic response is simulated since each eye exerts a symmetrical control.

Among worms, these reactions have been most closely studied in *Planaria maculata*, one of the turbellarian worms.¹ The normal individual orientates photo-negatively, illumination of one side producing a muscular contraction of the opposite side so that the worm proceeds directly away from the light. If, however, one eye is dissected out and the light is accurately directed or if different parts of the remaining eye are removed, it can be shown that stimulation of the elements of the anterior end of the eye makes the animal turn from the illuminated side, while stimulation of the posterior or ventral parts of the eye induces a turning towards the illuminated side. The boundary between these two constitutes the "line of fixation" (a functional fovea) stimulation of which evokes no turning movements (Lüdtke, 1942). A somewhat similar reaction is seen in the drone-fly, *Eristalis*, and related insects (Mast, 1923).



Turbellarian worm

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TELOTAXIS

In TELOTAXIS orientation is directly towards (or away from) the source of light ; there is no question of bilateral balance, nor, indeed, are two eyes necessary ; but it is essential to have an eye with several receptor elements which are able to appreciate the direction of a single light or each of several sources simultaneously, and a central nervous organization which can inhibit all stimuli except one. It is this factor of inhibition which forms the essential evolutionary advance, for it provides a mechanism much more efficient than is available to the previous types which respond to the summation of all stimuli (Figs. 28 to 31).

¹ Pearl (1903), Mast (1910-11), Boring (1912), Steinmann and Bresslau (1913), and particularly Taliaferro (1920).

THE EYE IN EVOLUTION

This type of response is characteristic of a large number of Arthropods, particularly Insects, in laboratory conditions; most of them react in a similar manner.¹ Whether flying or walking deprived of their wings, they proceed directly towards a light ; if two lights are

FIGS. 28-29.—TELOTAXIS IN THE BEE.

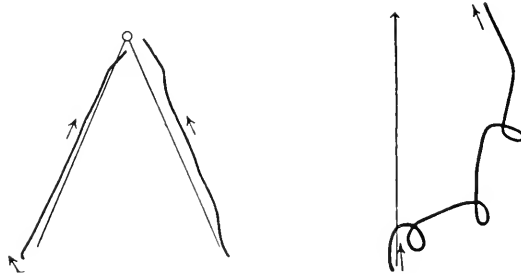


FIG. 28.

FIG. 29.

FIG. 28.—The tracks of two bees in a relatively straight line towards a light (indicated by the circle).

FIG. 29.—The path taken by a bee in a directive light (indicated by the arrow), when the left eye is blackened. There are some circus movements to the right initially, whereafter the insect eventually walks directly towards the light (Minnich, 1919).

FIGS. 30-31.—TELOTAXIS IN A TWO-LIGHT EXPERIMENT.

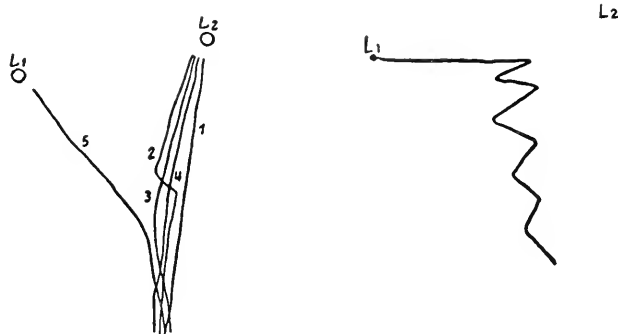


FIG. 30.

FIG. 31.

FIG. 30.—The tracks of 5 hermit crabs in their taxes towards two lights, L_1 and L_2 . Each part of the track is directed towards one light only. 1, 4 and 3 travel directly to L_2 . 2 does so initially and after a short time directs itself towards L_1 but rapidly resumes the path straight to L_2 . 5, after an initial start towards L_2 , travels straight towards L_1 (after von Buddenbrock, 1922).

FIG. 31.—The track of an isopod, *Aega*. For a time it follows a zigzag course alternating between L_1 and L_2 until it finally makes up its mind to travel straight towards L_1 (after Fraenkel, 1931).

¹ The blow-fly, *Calliphora vomitoria*—Rádl (1903); the aquatic nepid, *Ranatra*—Holmes (1905); the fruit-fly, *Drosophila*—Carpenter (1908); the butterfly, *Vanessa*—Dolley (1916); the robber-fly, *Erax rufibarbis*—Garrey (1918); the honey-bee, *Apis*—Minnich (1919), Clark (1928), Urban (1932); the drone-fly, *Eristalis*—Mast (1923), Dolley and Wierda (1929); the flesh-fly, *Sarcophaga*—Wellington (1953); the locust, *Locusta migratoria*, in the hopper stage—Chapman (1954); and others.

exposed they may take a zig-zig path initially, as if hesitating between the two, but soon the insect goes towards one, usually the stronger, neglecting the other (Figs. 30 and 31) ; and if it is unilaterally blinded, after some initial circus movements it again proceeds straight towards the light (Fig. 29). Experimenting with termite larvæ (*Calotermes*), Richard (1948) found that the direction of motion was determined by the direction of the rays rather than by the intensity gradient, but that the latter determined the straightness of the path. The

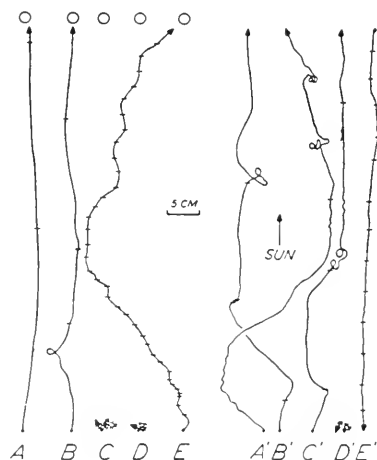


FIG. 32.—THE RELATIVE ROLE OF THE OCELLI AND COMPOUND EYES IN TELOTAXIS.

A, B, C, D, the track of the flesh-fly, *Sarcophaga*, in a darkened room towards a light indoors (6-watt lamp, marked by the circle).

A, a fly with all its eyes uncovered ; B, only the compound eyes uncovered ; C, only the ocelli uncovered ; D, all the eyes covered. It is seen that in C and D the insect is completely at a loss.

A', B', C', D'. Movements of the same individuals over the ground outdoors towards the sun. It is seen that the fly with only its ocelli uncovered orientates itself well. The irregularities of the tracks were produced by responses to patches of cirrus cloud passing overhead and do not occur when the sky is clear.

E. The track of the larva of the sawfly, *Neodiprion*, indoors, and E' outdoors. It is seen that, in contradistinction to *Sarcophaga*, the track outdoors is straighter than that indoors.

The time-marks in all tracks show 10-second intervals (W. G. Wellington, *Nature*).

stemmata of larvæ generally mediate this activity, but in the adult as a rule the effective organ is the compound eye, the action of which is frequently supplemented by the ocelli which, however, may be quite ineffective by themselves.

Fig. 32, for example, taken from Wellington's (1953) work, shows the phototactic response of the common dipterous parasite, the flesh-fly, *Sarcophaga*, crawling with clipped wings towards an ordinary (non-polarized) light in the

laboratory ; its path towards the light with all its eyes uncovered is straight ; with only its compound eyes uncovered, relatively straight ; and with only its ocelli uncovered, quite indeterminate.



Sarcophaga



Honey-bee



Mysid



Eupagurus



Photinus

The compound eye of the average adult insect is well equipped to respond accurately to a telotactic stimulus of this type, and may be specifically differentiated for the purpose. In the honey-bee, for example, the rapidity and accuracy of the response are due to the functional arrangement of this organ wherein tropotactic as well as telotactic elements are found ; the anterior median units of the eye (ommatidia) initiate reflex turning movements to the contralateral side, the lateral ommatidia to the ipsilateral side, while the central ommatidia, which alone are used for fixation, initiate none (Fig. 33). The animal is thus provided with a very efficient mechanism of orientation, the peripheral parts of which can initiate turning in either direction so that the stimulus is rapidly directed to the important central area, a reflex mechanism which is analogous to the fixation reflexes in man.

A more plastic mechanism is seen in some aquatic Crustaceans such as the tiny mysids of aquarium tanks (*Hemimysis*—Franz, 1911 ; Fraenkel, 1931) or the hermit crab, *Eupagurus* (von Buddenbrock, 1922 ; Alverdes, 1930). The latter animal goes towards a single light, and even although it continually changes its method of progression, now walking forwards, now sideways or at an angle, it invariably walks straight towards one light in the environment, a directness of path unaffected by the removal of one eye. It would seem that, unlike the bee, any part of the crab's retina can act as a fixation area, and that it must be endowed with a more plastic degree of visual coordination.

The orientation of the fire-fly, *Photinus pyralis*, is even more interesting (Mast, 1912 ; Buck, 1937). If a male glows¹ in the neighbourhood of a female, she raises and twists her abdomen so that its ventral surface is directed straight towards him no matter in which direction he may be, and produces a momentary glow ; he thereupon, no matter in which direction he is going, turns through any required angle between 0° and 180° towards the spot whence the glow came and proceeds in total darkness straight towards her. These responses, which

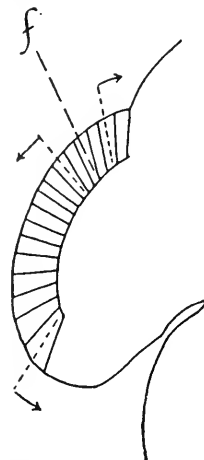


FIG. 33.—THE TELOTACTIC TURNING RESPONSE IN THE COMPOUND EYE.

When *f* is the line of fixation the arrows show the direction of turning induced by illumination of different regions of the eye (after Kühn).

¹ p. 742.

frequently occur when one eye only is illuminated, are directionally very exact and do not depend on the persistence of the stimulus—a primitive kind of menotaxis.

The execution of these movements of orientation in insects is the result of a complex series of coordinated reflexes in the wings or legs of both sides, each of which is specifically correlated to the location of the

FIGS. 34-36.—THE ORIENTATION OF THE ROBBER-FLY, *PROCTACANTHUS*, ON A WHITE BACKGROUND IN A HORIZONTAL BEAM OF LIGHT.

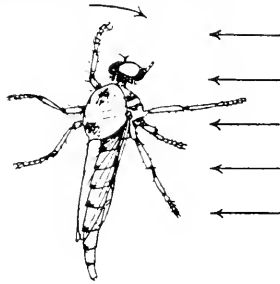


FIG. 34.—The upper portion of the left eye and the lower portion of the right eye are covered. The insect is leaning to the left and turning to the right towards the light.

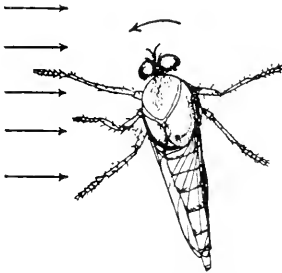


FIG. 35.—One leg has been removed on the right side while the light comes from the left. The insect is seen turning to the left towards the light guided largely by its left front leg.

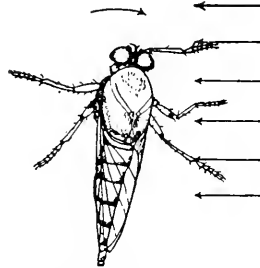
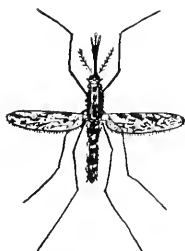


FIG. 36.—When the light comes from the right, in order to orientate itself in this direction, the left front leg is thrown over to the right side and is used to pull the animal in this direction (after Mast, 1924).

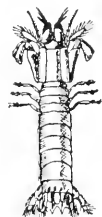
stimulus in the eyes. The excitation of a particular retinal area induces a reaction which orientates the insect in a direction such that the continuous turning allows successive retinal points to be stimulated until the fixation ommatidia are reached ; once this orientation has been attained, the reflexes become inoperative, and if any subsequent deviation occurs further reflex re-orientation immediately corrects it. These reflexes are somewhat analogous to the segmental scratch-reflexes in higher mammals, and their effects have been explored experimentally (as by rotatory experiments on a turn-table) in a large



Silver-fish



Mosquito



Gonodactylus

number of species by numerous observers.¹ If the insect is illuminated from in front, it steps forwards using all its legs; if from the side, the front legs on both sides step towards that side even if one eye only or parts of the eye are functional (Fig. 34); and if the front leg on one side is removed, on lateral illumination the front leg of the other side is extended towards the light, pulling the animal round towards the normal or, if necessary, the mutilated side so that it can orientate nearly as precisely as a normal insect (Mast, 1923-24) (Figs. 35 and 36).

SCOTOTAXIS (σκότος, darkness) is a term sometimes employed to describe the habit of some organisms, particularly insects, to travel towards a dark object: thus insects such as the silver-fish, the caterpillar, the ant, the mosquito and the louse² will travel towards a dark screen; if such a screen and a light are exposed, some will go directly away from the light (negative phototaxis) and some towards the dark screen (scototaxis).³ The stomatopod, *Gonodactylus*, which becomes more active in darkness, will always seek a dark shelter rather than a bright object even although it has to swim towards the light to get there (Bolwig, 1954). It is probable, however, that in most cases such behaviour can be included within the concept of negative telotaxis, although occasionally the form of a dark object may be important in the orientation.

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MENOTAXIS

So far we have considered orientations either directly, or relatively directly, towards or away from a source of light; it is obviously of greater biological importance if, in addition, *an animal can travel at an*

¹ Rádl (1903), Santschi (1911), Wolf (1927-31), Fraenkel (1927), Schulz (1931), v. Buddenbrock and Schulz (1933), and others.

² *Lasius*—Meyer (1932); *Vanessa*—Götz (1936); *Lasius*—Weyrauch (1936); *Aedes*—Kennedy (1939); *Culex*, *Anopheles*—Rao (1947); *Pediculus*—Wigglesworth (1941).

³ *Formica*—Klein (1934).

angle to the light, thereby putting itself in the position of the pilot of a ship who can steer otherwise than directly in line with the sun or the pole-star. In the simpler types of orientation, light acts as a stimulus attracting or repelling the animal into a more favourable environment ; in menotaxis light is merely used as a means to an end, guiding the animal to a place where it wishes to go whether favourable or not.

Four types of response which can be considered as menotactic (the term being used in its widest sense) require particular note—the light-compass reaction, orientation to polarized light, orientation to a visual pattern, and the dorsal (or ventral) light reaction.

The LIGHT-COMPASS REACTION, whereby the animal travels at a fixed angle to a light (the ORIENTATION ANGLE) either in a straight or a circular direction, was first described by Santschi (1911) in his observations on ants,¹ and was so named by von Buddenbrock (1917) (Lichtkompassbewegung) (Fig. 37). It is a response of considerable complexity and of wide distribution, occurring in some polychaete worms,² in some molluscs,³ in the Amphipod, *Talitrus saltator*,⁴ in spiders returning from a kill in the centre of their web,⁵ in a large number of insects returning to their nests,⁶ and in some birds as a means of navigation.⁷ In general, light-compass reactions may be divided into two types. In the first (TROPO-MENOTAXIS, Ludwig, 1934), the reaction is essentially simple and tropic in type, being governed primarily by the intensity of the light, and if two lights appear, their effects are summated and the animal orientates itself balanced at an angle between them⁸ ; but the more common reaction is one of TELO-MENOTAXIS wherein the receptor organ is sufficiently evolved to appreciate the direction of a light and is able to inhibit other stimuli so that it can orientate itself with reference to it alone.

The orientation of the Mollusc, *Elysia viridis*, with respect to light. α is the orientation angle which the longitudinal axis of the Mollusc makes with the direction of the light (Fraenkel).

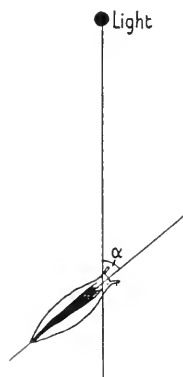


FIG. 37.—
MENOTAXIS.

There is no doubt that in laboratory conditions and with controlled artificial sources of light many Arthropods show a remarkably high degree of accuracy in maintaining an orientation angle by this means ;



Web spider



Geotrupe

¹ p. 68.

² v. Buddenbrock (1937).

³ The common snail, *Helix*—v. Buddenbrock (1919) ; the Mediterranean Gastropod, *Elysia*—Fraenkel (1927).

⁴ Pardi and Papi (1953).

⁵ Bartels and Baltzer (1928), Bartels (1929), v. Buddenbrock (1937).

⁶ v. Buddenbrock (1931–37), v. Buddenbrock and Schulz (1933).

⁷ Ruppell and Schein (1941), Lack (1943), Wilkinson (1949), Matthews (1951–53).

⁸ The caterpillars of the gipsy moth, *Lymantria dispar*—Ludwig (1934) ; the dung beetle, *Geotrupes sylvaticus*—Honjo (1937).

the Amphipod, *Talitrus saltator*, for example, reacts in this way to the moon (Pardi and Papi, 1953). Until recently most writers agreed that this reaction was the essential factor in the orientation of insects out-of-doors. This is probably the case when fog or cirrostratus turns the sun into a small light source, but the lack of consistency in the behaviour of insects in natural conditions when the sun is bright does not substantiate that this is the main or even an effective mechanism, and the experiments of Wellington (1955) would seem to indicate that solar heat and the response to the plane of polarization of light¹ are the essential factors in determining their conduct in these circumstances.

The accuracy of the response of the light-compass reaction in insects is made possible by the structure of the compound eyes, for

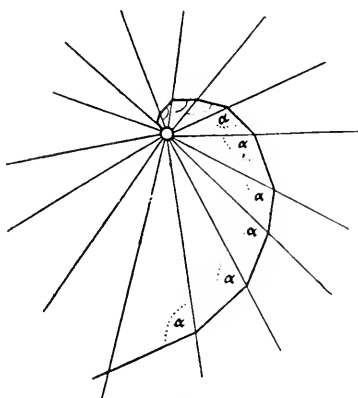


FIG. 38.—MENOTAXIS.

The insect moves so that its course makes a constant angle (α) with rays of light issuing from a source; it therefore approaches the source along a logarithmic spiral (after von Buddenbrock).

they orientate themselves in such a way that the sun's rays stimulate one or at most a few ommatidia all the time.² The high degree of accuracy thus obtained may be gathered from the fact that insects sometimes correct their angle of orientation if the light merely passes from one ommatidium to its neighbour (von Buddenbrock and Schulz, 1933). When the guiding light is sufficiently far away this type of response is effective in orientating the insect in a straight line, but if the stimulus is close an entirely different result is seen. If the insect were to pursue a straight path, the incidence of such a light on the retina would constantly change; and if the angle of incidence is to be kept constant, the insect must perforce turn along a logarithmic spiral which ends in the light itself (Fig. 38) (von Buddenbrock, 1937). Caterpillars crawl to a light in this type of spiral path (Ludwig, 1933-34) and it is for this reason that the moth, applying a mechanism adapted

¹ p. 73.

² p. 174.

for reference to a distant source of light, flies to its death in the nearby flame.

This behaviour is not constant in moths. If a number of these insects is introduced into a room where a candle is situated on a table they will take up positions on the table around the light with their heads turned towards it. As a rule, one by one they take wing: the first may fly around the flame in diminishing circles until it passes through it to fall in flames into the molten mass of wax beneath; the next will similarly follow to commit deliberate suicide; and so on the procession goes, some perishing in the flame itself, others escaping with singed wings to fall on the table when, with wings too charred to use, they may crawl with difficulty up the candle and walk straight into the base of the flame to die. While most fly around the flame in decreasing circles, some may fly straight into it; others remain upon the table apparently worshipping from afar, while others again wander aimlessly about the room paying no attention to the light. The cause of this variation in conduct is quite unknown; it seems to indicate that the phototactic response is not entirely determined on a mechanistic level.

The navigational sense in birds is an astonishing example of the accuracy of a modification of the light-compass reaction. It has long been known that young birds will undertake their initial migration from one continent to another unaccompanied by their parents and arrive in the correct habitat with extreme precision, and that homing birds such as the pigeon or the gull, released in an unknown area in random directions, will rapidly head straight for home in a direct line of flight (Matthews, 1951-55; Kramer and St. Paul, 1952; Kramer, 1953). The Manx shearwater, *Puffinus*, for example, transported to America, has homed 3,050 miles across the Atlantic wastes to arrive after 12½ days in its own particular burrow on an island off the west coast of England (Matthews, 1953). It is obvious that in navigational feats of this type visual orientation is quite inadequate and a bi-coordinate orientating mechanism of great accuracy must exist. It is true that many birds show a relatively simple positive phototactic response, flying towards an illuminated patch or the lighted end of a long dark tunnel—a primitive reaction still carried out after ablation of the cerebral hemispheres (pigeons, Viaud and Marx, 1948); but it is equally true that they are capable of executing the most complex type of orientation.

For years this navigational ability of some birds has excited the curiosity of naturalists. Several explanations have been explored such as an acceleration-displacement recording mechanism or an ability to exploit the earth's magnetic field, but they have all been discredited by experiment¹; nor do the structural arrangements apparently exist in the eyes of birds as in the compound eyes of insects to appreciate the



Puffinus

¹ Gordon (1948), Matthews (1951-55), Yeagley (1951), van Riper and Kalmbach (1952).

polarization pattern of the sky (Montgomery and Heinemann, 1952). The evidence would seem incontrovertible that these birds can orientate themselves by an innate ability to estimate the sun's arc by observation of its movement over a small distance and, by extrapolation, to navigate automatically over great distances with extreme accuracy even when flying is continued during the night. Flight throughout the journey is governed by a number of factors developed by individual experience in respect of which considerable variations exist, but the fundamental basis of the method of orientation is an innate form of sun-navigation depending on an appreciation and memory of the angle of incident light and an ability to make appropriate corrections according to the 24-hour rhythm of a reference system (an internal clock) operating in the brain (Ruppell and Schein, 1941; Lack, 1943; Saint Paul, 1953; Matthews, 1953-55; Kalmus, 1954; Pratt and Thouless, 1955).



Homing pigeon

This theory had its origin in the observations of Ising (1945), Varian (1948), Davis (1948) and Wilkinson (1949), but the most satisfying evidence came from the experiments of Matthews (1951-55) on homing pigeons, gulls and Manx shearwaters. He found (as have others) that birds released in a strange or clueless environment (such as over the sea) rapidly orientated themselves in the correct direction for home as they soared to fly, and maintained their direction over long, direct flights over unknown country; but they were able to find the correct direction only when the sun was up and their initial accuracy in flight depended on a clear sky; in cloudy or overcast weather they were helpless

FIGS. 39-40.—NAVIGATION BY BIRDS.

To illustrate the initial orientation of the Manx shearwater when released in a strange environment. The home direction is vertically upwards. The length and breadth of the rays is proportional to the number of birds that orientated in the direction indicated.



FIG. 39.

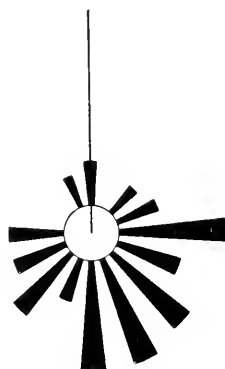


FIG. 40.

FIG. 39.—Orientation under a cloudless sky. It is seen that the great majority of the birds orientated themselves initially in approximately the right direction.

FIG. 40.—Orientation under heavily clouded skies. The ability to orientate correctly has been lost (G. V. T. Matthews).

(Figs. 39 and 40). By keeping the birds in conditions wherein the sun and sky were excluded for a number of days before release, consistent errors were made which could only be explained on the supposition that the birds were failing to correct for the seasonal variation in the sun's altitude from which they derived their measurement of latitude. By de-synchronizing the day-night rhythm before release by arranging an artificial day beginning and ending a few hours earlier or later than normal, errors in longitude were made which could be explained on the basis of a disturbance of an inherent time-sense based on

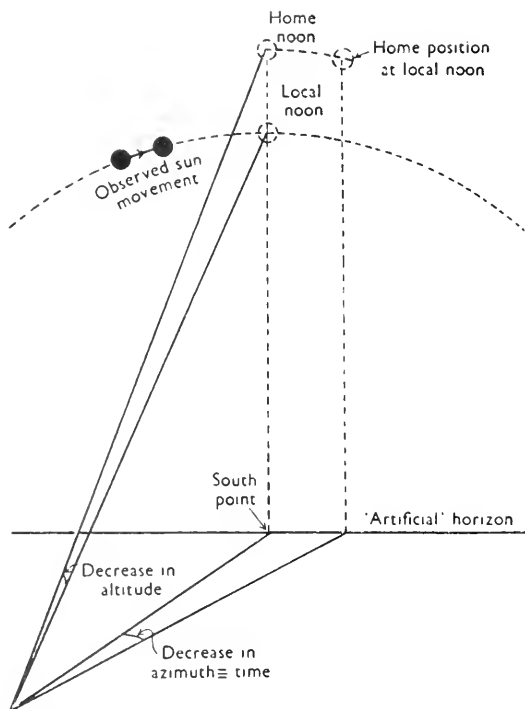


FIG. 41.—DIAGRAM ILLUSTRATING THE HYPOTHESIS OF SUN NAVIGATION. Released to north and west of home. See text. (The diagram is not to scale.) (After G. V. T. Matthews.)

regular light-dark sequences; they flew in a false direction—too far east after an advanced day, too far west after a retarded day. That the direction is determined by the incident light was strikingly shown in Kramer's (1952) experiments with migrating starlings: when the light was deflected by 90° by mirrors, the birds' flight was equally deflected and in the same direction.

Wilkinson's hypothesis is illustrated in Fig. 41. Briefly, the sun's arc is observed over a small excursion and from this its position at local noon and the geographical south are extrapolated; the latitude is determined by the difference between the observed noon altitude and the remembered noon altitude at home. The difference in longitude is derived partly by comparison with the home position in azimuth at local noon combined with an estimation of time in the diurnal night-day cycle. This, although it is not yet experimentally

proven, appears at present to be the most probable explanation of the observed facts ; it may well seem so complicated an automatic calculation by a creature with a proverbially small brain as to appear fantastic ; but the ability of a bird released in America to orientate itself immediately for its flight to a particular and very precise locality in Europe is fantastic—it occurs within 40 seconds of viewing the sun. It would seem that on the basis of its structural potentialities, the avian retina should be capable of such a feat.¹ It has also been suggested (again without proof) that the pecten² may play some part in the analysis by acting as a fixed point when taking observations (Menner, 1938 ; see also Crozier and Wolf, 1943 ; Griffin, 1952).

ORIENTATION TO POLARIZED LIGHT. Arthropods as widely different as the king-crab, the sand-hopper, the ant and the honey-bee possess the ability to respond to the plane of polarization of light, and by this means may orientate themselves in skylight out-of-doors. This faculty can be investigated experimentally by observing the response to the rotation of the axis of a sheet of "Polaroid" glass. Sensitivity of this type was first demonstrated in bees by von Frisch (1949) and has since been confirmed in behavioural experiments involving a number of Arthropods, both larvæ and adults,³ and has also been proved by electroretinographic responses.⁴

Light from the blue sky (not directly from the sun) has been scattered from particles in the atmosphere which also partly polarize it, that is, more of the light-waves vibrate in one transverse direction than in others. The plane of maximum polarization is different for each patch of blue sky, and the proportion of light polarized also varies, being greatest at 90° from the sun. Thus each patch of blue sky has its own plane and intensity of polarization, differing from every other patch. A "Polaroid" glass is a submicroscopic crystalline grid transmitting chiefly light vibrating in one particular direction ; it can be used to analyse the plane and intensity of polarization of light since, on rotation, light polarized in other planes is cut off.

We shall see presently⁵ that insect larvæ have simple eyes (stemmata) while adults, in addition to simple eyes (ocelli) are usually equipped also with two large compound eyes. The stemmata of the larvæ respond both to direct light and alterations in the plane of polarization, while in adults the ocelli sometimes show little or no phototactic response to non-polarized light, but aid the compound eyes in their response to polarized light. In these cases the former are thus supplementary in function so that the intact animal reacts more quickly and accurately than one deprived of its ocelli.

¹ p. 417.

² p. 416.

³ Larvæ of the sawfly, *Neodiprion*—Wellington *et al.* (1951) ; mosquito larvæ—Baylor and Smith (1953) ; adult insects—Vowles (1950–54), Menzer and Stockhammer (1951), Carthy (1951), Stephens *et al.* (1952–53), Wellington (1953), de Vries *et al.* (1953) ; other Arthropods—Waterman (1950), Kerz (1950), Pardi and Papi (1952), Baylor and Smith (1953), and others.

⁴ Autrum and Stumpf (1950). Waterman (1950–51).

⁵ p. 222.

The interesting experiments of Wellington (1953) will make the matter clear. Fig. 42 shows the abrupt changes of direction associated with rotation of the axis of a sheet of "Polaroid" held over larvæ crawling over the ground; the intact animal responds most markedly, but an adequate response is obtained if either the ocelli or the compound eyes are functioning alone.

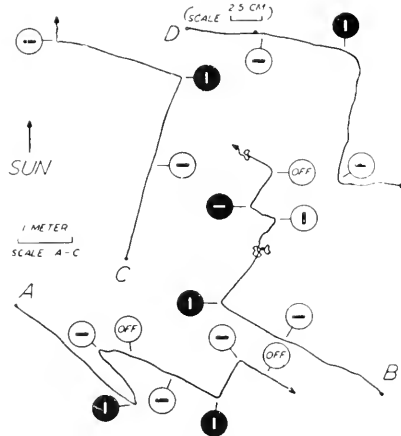


FIG. 42.—THE EFFECTS OF ALTERATIONS IN THE PLANE OF POLARIZATION ON THE ORIENTATION OF INSECTS.

The plane of polarization was changed by rotation of the axis of a sheet of "Polaroid" held between the insect and the sun as it crawled over the ground. The circles show the point at which the sheet of Polaroid was placed over the moving insect or rotated or withdrawn. The bar inside the circles shows the orientation of the axis with respect to the sun, and the shading of the circle indicates whether or not the sky was appreciably darkened when viewed through the "Polaroid" with the axis set as shown.

A, B, C. The path of a fly: A, with all its eyes functioning; B, with only its compound eyes uncovered; C, with only its ocelli uncovered.

D. A fourth-instar larva of *Neodiprion* (drawn on a different scale).

The marked convolutions in the path of B show the response to alterations in the polarization of the skylight when a patch of cirrus cloud passed overhead (W. G. Wellington, *Nature*).

The Orientation of Insects out-of-doors

It would thus appear that the orientation of insects in natural conditions in daylight is a very complicated matter. When these questions first received attention in the classical observations of Santschi (1911) and Brun (1914) on the behaviour of the ant,¹ its conduct was interpreted as being regulated by a light-compass reaction alone. At a later date the experiments initiated by von Frisch (1949-51) introduced the complicating factor of a response to the plane of polarization of light. Finally, the experiments of Wellington and his co-workers (1953-55) have stressed the importance of a thermal response. There is complete agreement that the light-compass

¹ p. 68.

reaction is the essential determinant of behaviour in laboratory conditions with artificial light, in natural surroundings at night and in circumstances during the day when the sun is largely obscured, but these latter workers believe that on a clear day the sun acts primarily as a source of heat. Wellington (1955) concluded that in full sunlight, insects in open places orientate themselves primarily by solar heat when it is available and maintain their orientation to the sun or their straight-line travel in its absence by polarized light from the overhead sky; if as may happen when smoke or cirrus cloud of varying densities passes overhead, the plane of polarization changes rapidly, the response may completely break down and the insect remains stationary even although the sun remains exposed (see Fig. 32). This sometimes makes its behaviour appear irregular and difficult to interpret, particularly in the neighbourhood of industrial centres where haze and smoke are plentiful. Wellington considered that during overcast weather travel is probably also aided by light gradients (tropo-menotaxis). In general, when an insect is cool it is thermo-positive and travels towards the sun; when it is warm it is thermo-negative and orientates itself away from the sun, and if it becomes overheated and the plane of polarization changes rapidly the insect becomes disorientated and is incapable of travelling so that it often circles aimlessly until it succumbs to heat-stroke (Wellington *et al.*, 1951-54; Sullivan and Wellington, 1953; Wellington, 1955). The same complex interaction between thermal and visual stimuli is seen in the locust which postures at right angles or parallel to the sun's rays depending on the temperature (Volkonsky, 1939). Occasionally, as in the ant, the evidence suggests that other stimuli such as gravity are also effective in orientation in such a way that the geotropic and phototactic elements are correlated in a single central mechanism of taxis (Vowles, 1954).



Ant

From the historical point of view, the *homing of the ant* provided the classical example of this type of activity. The purposive behaviour of these insects, particularly when returning to the nest laden with

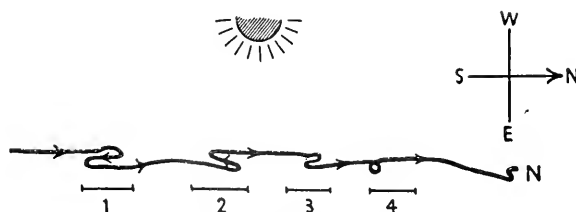


FIG. 43.—MENOTAXIS.

The ant was returning to its nest, N, with the sun on its left side. On four consecutive places, 1, 2, 3 and 4, it was shaded from the direct light of the sun and the image from the sun was projected from the animal's right by means of a mirror. On each occasion the animal preserved its initial orientation relative to the sun or its image by turning round (Santschi).

food, in spite of an immense load between their mandibles and in face of all obstacles, has excited admiration and conjecture for centuries. Nevertheless, although considerable intelligence is suggested, the response is largely automatic. Cornetz (1911) observed that if such an insect were lifted up and set down in another place, it set off in the same direction as before whether or not this led to the nest. That the directing influence was the sun was shown by Santschi (1911) who shaded the ant from the sun and deflected its rays by a mirror so that they reached the insect from the opposite side; each time this was done the ant immediately changed its path so that it maintained the same direction with regard to the reflected rays as it had previously to

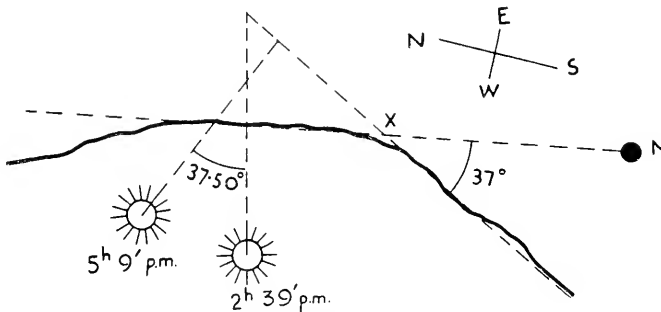


FIG. 44.—MENOTAXIS.

The orientation of the ant, *Lasius niger*. The dark line indicates the route taken by the ant towards its nest, N. The initial part of its journey was orientated at an angle of about 90° to the sun. At X, the ant was imprisoned in a box for $2\frac{1}{2}$ hours, from 2.39 p.m. to 5.9 p.m. During this time the sun had traversed an angle of 37.5° . On its release, the ant resumed its path again at right angles to the late afternoon sun, deviating from its former path by an angle of 37° (after Brun).

the direct rays (Fig. 43). The same reaction was demonstrated in locusts by Kennedy (1945–51), who found that the direction of the marching desert hoppers could readily be changed and that of flying adults momentarily changed by reflecting sunlight onto them with a mirror. At first this response was assumed to be a typical example of the light-compass reaction, but Wellington (1955) brought forward evidence that it was more probable that radiant heat associated with the reflected light was the more effective stimulus.

A still more elaborate response was demonstrated in the classical experiment of Brun (1914) who confined an ant in a box for some hours in the middle of its homeward journey to its nest; on releasing the insect it set out on a new track, not now towards its nest but deviating from its original route by an angle corresponding to that through which the sun had moved in the interval so that its rays were still received at the same angle as before (Fig. 44). Again, this was initially

taken to be an example of the light-compass reaction, but the response could be equally explained by orientation by the pattern of polarization which also shifts with the sun (Griffin, 1953 ; Wellington, 1955). The homing of the honey-bee when deprived of other optical clues such as conspicuous landmarks¹ is determined by the same mechanism (Wolf, 1927 ; von Frisch, 1931). Behavioural experiments have demonstrated that certain insects are not only able to analyse the polarization of light but can retain its pattern in their memory to take account of the alteration in the position of the sun with the time of day (von Frisch, 1950 ; Vowles, 1950 ; Griffin, 1950 ; Stephens *et al.*, 1952) ; by this type of mnemotaxis it is probable that homing remains accurate for long journeys despite the changing position of the sun.

It is not to be thought, however, that the homing of the ant need be an entirely visual process. Bonnet (1779-83) first showed that odour trails may be an effective aid (Carthy, 1950 ; Vowles, 1955), and the ability of this insect to improve its path-finding and avoid detours is exemplified in its extraordinary capacity to learn quite complex mazes (Turner, 1907 ; Schneirla, 1929-33 ; etc.).

It is interesting that the "*dancing*" of bees, the ballet by which they communicate to other foraging bees the direction, the distance and the richness of a discovery of nectar, is also largely determined by the

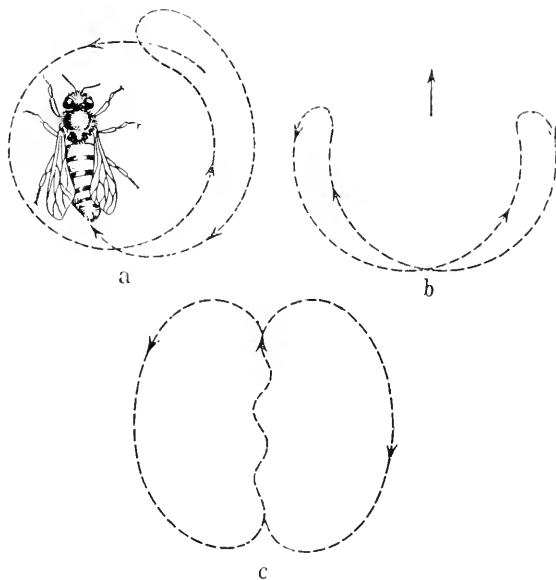


FIG. 45.—THE DANCE-FIGURES OF BEES.

(a) The round dance for short distances performed by German and Austrian bees. (b) The "sickle dance" for short distances performed by Dutch and Swiss bees. (c) The figure-of-eight dance for long distances, with the "waggle-run" forming the central component of the figure (von Frisch).

¹ p. 78.

polarization pattern reflected from the sky. The coordinated dance which a returned forager performs on the surface of the comb within the hive was described by Aristotle,¹ and in recent times has been most closely studied by von Frisch,² the Austrian naturalist (1949-54), using slow-motion cinematography and specially marked bees attracted to rich diets placed at different distances in different directions from the hive. For distances closer than 10 metres the returned bee communicated its news to the rest of the hive by performing a simple circular dance; for distances greater than this the direction of the food is indicated by using the vertical direction on the surface of the

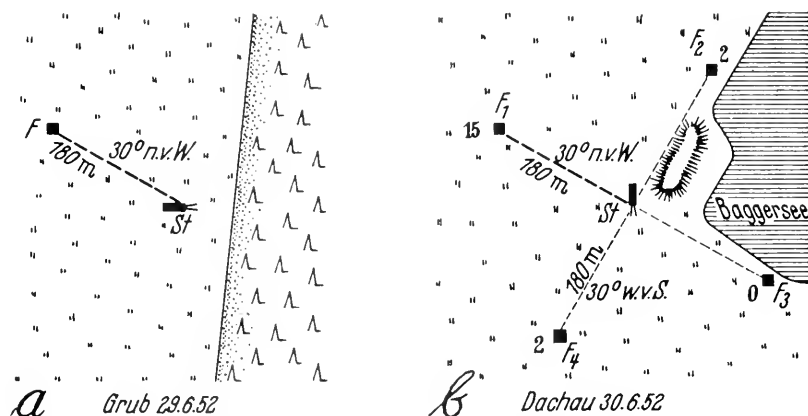


FIG. 46.—THE "DISPLACEMENT TEST" IN THE ORIENTATION OF THE BEE.

This test indicates the ability of the honey-bee to allow for a change in the position of the sun. In (a), marked bees from a hive, *SL*, were allowed to feed on the afternoon of June 29th, 1952, from a feeding place, *F*, 180 m. away in the direction 30° north of west. The following morning the hive was transported to another entirely unknown landscape of a completely different type. The vast majority of the bees (15 out of 19), without any help from familiar landmarks, went to one of 4 alternative feeding places 180 m. away from the hive and 30° north of west, ignoring other symmetrically placed feeding places. On the first afternoon the sun had been in the west; on the second morning the sun stood in the east; so that in order to retain the same orientation the bees must have been able to calculate and allow for the solar movements (von Frisch).

comb (the direction of gravity) to represent the direction of the sun's rays outside the hive, the distance of the source of food by the speed of the dance, and the richness of the find by its vigour. The dance takes the form of a squat figure-of-eight, the straight transverse run of which is marked by the bee actively wagging its body with an enthusiasm depending on the richness of the nectar (Fig. 45) ; the direction of this run bears the same relation to the vertical as does the position of the

¹ *Hist. Animal.*, 18, 624b, 8. See Haldane, *Behaviour*, **6**, 256 (1954).

² See Fig. 728.

source of food to the position of the sun at the time, while the speed of the dance varies inversely as the distance (about 10 revolutions in 15 secs. to indicate a distance of 100 metres, 2-5 revolutions to indicate 3,000 metres). The indications of direction attain an accuracy of 3° in good conditions, of distance of up to 100 metres. Moreover, unlike the ant, bees possess an innate time-keeping mechanism whereby they can make compensation for the movements of the sun or changes in the pattern of polarization in the sky as the day progresses, making the appropriate correction in their direction (Fig. 46).

It is interesting that there is no component in the dance for a vertical distance, presumably because such is rarely required in natural surroundings; and when von Frisch *et al.* (1953) fed bees on a feeding-table perched on a radio beacon directly above the hive, new foragers were unable to find it. As performed in the hive the waggle-run serves to indicate the direction of the food as related to the sun by reference to the vertical as determined by gravity; occasionally the dance is performed on the horizontal alighting board in front of the hive and in this case the waggle-run points to the actual direction of the feeding place without reference to the sun. Moreover, in different localities different "dialects" are used. Thus, while von Frisch (1950) found that Austrian and German bees dance in a circle to indicate food near at hand without giving any indication of its direction, Tschumi (1950) and Baltzer (1952) found that Swiss bees, and Hein (1950) that Dutch bees perform a "sickle dance", dancing in a semi-circle the axis of which denotes the appropriate direction to be followed exactly in the same way as the straight part of the figure-of-eight dance indicates this for far distances (Fig. 45b).

This extremely complex and highly ritualized pattern of behaviour is an astonishing performance, particularly when it is recalled that the brain of the bee is about one-tenth of an inch in diameter; it is apparently inborn and instinctive, but its precise implications have to be learnt through experience by the young workers (Lindauer, 1952). The response is disorientated in shadow, resumes its rhythm as soon as a patch of blue sky becomes visible, and can be artificially changed by the interposition of a polarizing film between the insects and the sun. Moreover, when trained bees are transported from the northern to the southern hemisphere where the direction of the sun's movement to an observer is anti-clockwise instead of clockwise, their foraging movements tend to be reversed (Kalmus, 1956). A somewhat similar or even more complicated "language" is used by scout bees to indicate the position or direction for a suitable new home or swarm.

It is clear, therefore, that the orientation of insects out-of-doors, although determined by automatic responses, is an extremely complex affair influenced by many stimuli acting sometimes singly, sometimes in combination; and it is equally clear that much work will require to be done before their behaviour is fully elucidated.

Aquatic Arthropods also make use of polarized light to orientate themselves while swimming, in some cases reacting to the polarized

light of the sky, as do Amphipods when seeking their return to the sea (Pardi and Papi, 1952-53), or making use of the polarization patterns which exist between the air-water interface (Waterman, 1954). Such reactions have been demonstrated in 12 species of Cladocera, water-mites and caddis-fly larvæ, which tend to swim so that their direction of movement is at right angles to the plane of polarization (Baylor and Smith, 1953). The crab, *Eupagurus*, shows a definite response to a change in the direction of polarization (Kerz, 1950) as also do mosquito larvæ.

*Eupagurus*

The navigation of the small crustacean, *Talitrus saltator*, as recorded by Pardi and Papi (1952-53) is a fascinating story. These Amphipods normally live in the intertidal zone. Transferred inland, they move towards the coastline whence they came, taking their direction from the angle of the sun; as with insects and birds their course can be deflected by changing the direction of the incident light by a mirror. If direct sunlight is not available they can orientate themselves by polarized light from patches of blue sky and can be similarly deflected by the interposition of a polarizing sheet; under a completely overcast sky they are disorientated. As with bees there is also an innate mechanism which allows them to compensate for movements of the sun throughout the day, but, unlike the reactions of the bee, it would seem that the whole mechanism is established by heredity or acquired in early youth and is set in each individual for ever and cannot be changed. Thus specimens on the west coast of Italy move westwards towards the sea, and even when brought to the seaside of the east coast will automatically attempt to travel westward right across country away from the nearby water. The most extraordinary thing about these creatures is that travelling through the night they appear to be able to navigate with reference to the moon. This is the only instance where this has been established and in view of the complication and rapid change of the lunar path across the sky, it would seem to be an extraordinary feat.

*Talitrus saltator*

ORIENTATION TO A VISUAL PATTERN so that its reception on the retina remains constant corresponds closely in its mechanism to orientation with respect to a source of light. Thus insects placed on a turn-table facing a window will move round when the table rotates (Rádl, 1902) and if a striped drum is rotated in front of them they will endeavour to keep in line with a given stripe (an "optomotor response") (Schlieper, 1927; Schulz, 1931; Zeiser, 1934)¹. Gregariousness in locusts depends on the same reaction; moving so that it nullifies the movement of images across its retina, each swarming insect travels precisely with its neighbour ("gregarian inertia"), the whole host being guided by a light-compass reaction to the incidence of the sun's rays (Kennedy, 1939-45). Orientation when swimming against a current of water ("rheotaxis") is in fact a visual response of the same type: the water-boatman, *Notonecta*, for example, turns upstream and swims with sufficient strength to maintain a constant impression of the nearby bank; if the landmarks on the bank are moved, the water-



Locust

*Notonecta*

¹ This reaction has been used to measure the visual acuity of insects, see p. 588.



Gyrinid beetle

boatman moves with them, and if they are obliterated as when swimming in the dark or between plain white boards, the insect allows itself to be carried passively downstream (Schulz, 1931). Gyrinid beetles are similarly disorientated when swimming in the dark or if a sudden change is made in the landmarks on the banks (Brown and Hatch, 1929).



Dragon-fly

THE DORSAL (VENTRAL) LIGHT REACTION. The orientation of animals which progress on the earth's surface can be treated as if movement on one plane only need be considered; but those that swim or fly have three available planes of movement—they can turn as do land animals on a vertical axis, but they can also roll on a longitudinal axis or they can pitch, turning somersaults about a transverse axis (Fig. 48). They must therefore possess a complex means of orientation to maintain the body in a desired position as it travels towards a goal. Because of its relatively greater specific gravity the stability of an animal body in air is greater than in water, and since the attachments of wings are comparatively high making the centre of gravity relatively low, the equilibrium of balance in birds raises no serious difficulties. This does not apply with the same force to insects although some, such as the dragon-fly, *Anax*, demonstrate a dorsal light response during flight, the effective organ being mainly the compound eye (Mittelstaedt, 1950); but aquatic animals require to perform constant and active balancing movements to maintain their normal orientation. Many fishes maintain their position optically by keeping one surface (usually the dorsal) perpendicular to the light, using their eyes as receptor organs; others have evolved a specific statocyst organ to maintain equilibrium, but although this development has assumed the greater importance eventually, the eyes still participate in the orientating reflexes, a collaboration between the senses which survives in the elaborate reflex connections which continue to yoke the visual with the vestibular system in Man.

*Daphnia*

The dorsal light reaction was initially recognized in the crustacean, *Daphnia*, by Rádl (1901), and its wide distribution was first appreciated by von Buddenbrock (1914-37); it has since been observed in many groups of aquatic animals of a wide variety.¹ In its essentials the DORSAL LIGHT REACTION ensures that when the light is above, the animal swims with the dorsal surface upwards, maintaining itself symmetrically to it and moving (if it does move) in a plane at right

¹ In Medusæ—Fraenkel (1931); polychæte worms—Fraenkel (1931), v. Buddenbrock (1937); in a large number of Crustaceans—v. Buddenbrock (1914), Alverdes (1926-30), Schulz (1928), Seifert (1930-32); among Insects in nymphs and larvæ—v. Buddenbrock (1915), Wojtusiak (1929); in the dragon-fly, *Anax*, during flight—Mittelstaedt (1949); perhaps in the desert locust, *Schistocerca gregaria*—Rainey and Ashall (1930); and particularly in Fishes—v. Holst (1935).

angles to it ; if the light is placed horizontally the animal rotates correspondingly, and if the light is placed below, it either rolls or somersaults over to swim belly-upwards (Fig. 47). In the VENTRAL LIGHT REACTION an animal which normally swims belly-upwards behaves analogously (Fig. 48). Occasionally, however, if the normal direction of the incidence of the light is changed, the animal does not

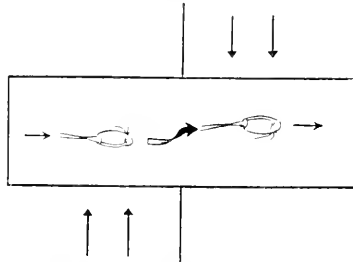


FIG. 47.—THE DORSAL LIGHT REACTION.

On the left half of the aquarium the Crustacean, *Apus*, is illuminated from its right side; on the right half of the aquarium, from its left side. As it swims between the two, it orientates itself by rolling on its longitudinal axis (after Seifert).

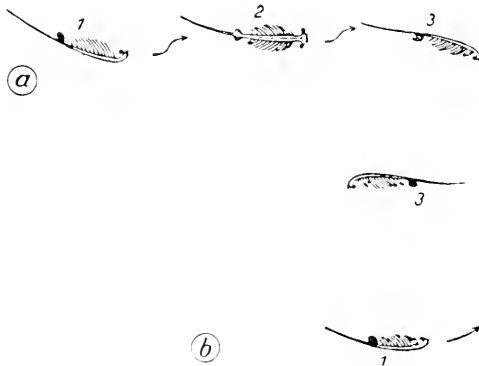


FIG. 48.—THE VENTRAL LIGHT REACTION.

The change of orientation in the Crustacean, *Artemia salina*, when the light is changed from above to below. Fig. 48a, by a rolling movement ; Fig. 48b, by a back somersault or pitching movement (in a photo-positive individual) (after Seifert).

act reflexly but becomes completely disorientated and swims aimlessly, a reaction seen, for example, in the nemertine worm, *Lineus ruber*, which in normal circumstances is negatively phototactic (Goutcharoff, 1952).

The visual mechanism involved varies in different species. In some larvæ the response is mediated by the dermal light sense and persists after total blinding (Schöne, 1951) but as a rule the eyes are



Lineus ruber



implicated. The water-flea, *Daphnia*, orientates itself in the typical manner by means of a single dorsal median eye ; while the fresh-water crustacean, *Apus*, has two compound eyes and a median eye on the dorsal surface. Other crustaceans have two eyes ; when one is removed or painted over, rolling and circling movements occur towards the seeing side, and if both are thrown out of action the light reaction disappears (the brine-shrimp, *Artemia*, Seifert, 1930-32).

The relation between the statocyst and the eyes in those animals which possess the dual mechanism was prettily shown by von Holst

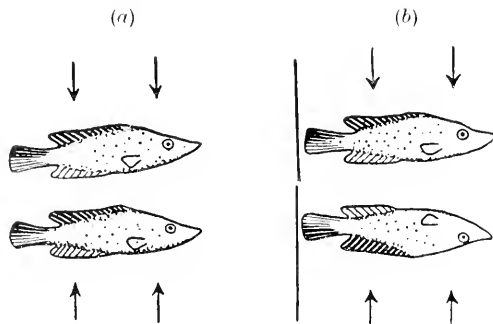


FIG. 49.—THE DORSAL LIGHT REACTION.

In the fish, *Crenilabrus rostratus*.

Upper two fish. The light comes from above ; (a) in the intact animal, (b) in the labyrinthectomized animal. Orientation is normal.

Lower two fish. The light comes from below ; (a) the normal posture is retained owing to the influence of the labyrinth ; (b) the labyrinthectomized animal swims in an upside-down posture (after von Holst).

(1935) in the fish, *Crenilabrus rostratus*. Normally the balance is maintained essentially by the static reactions of the labyrinth which are supplemented by the light reaction. If, however, a light is placed horizontally, a compromise orientation is assumed with the body slightly tilted towards the light, the inclination varying directly with the strength of the illumination ; when the light is placed underneath, the static reactions control the animal and the light is without effect (Fig. 49). When, however, the labyrinths are put out of action, the optical reaction functions in the pure form, the movements of the trunk, the fins and the tail, hitherto controlled by the labyrinth, now being entirely coordinated by the eyes so that with a transverse light the fish swims on its side ; with a light below, upside-down ; finally, when one eye is put out of action, the fish rolls towards the seeing side for a time until an adaptive reaction asserts itself.

This reaction, of course, is often combined with other types of phototaxis. Thus the water-flea, *Daphnia*, is usually positively tropotactic and also exhibits a compass reaction (von Frisch and Kupelwieser, 1913 ; Eckert, 1938), the brine-shrimp, *Artemia*, may be positively or negatively phototactic, and so on.

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MNEMOTAXIS

MNEMOTAXIS is the most complicated method of orientation and allows the animal to deal with all the elements of a complex situation in the light of experience gained in the past (Kühn, 1919-39). In the previous reactions we have studied, the response is made to one stimulus only or the synthesis of several, and it may be either direct as in tropotaxis or indirect as in menotaxis, a simple mechanism which becomes effective by the inhibition of all stimuli but the dominant one. These more primitive taxes determine the reactions of lower species, and although they enter into the total response of the higher animals and can be studied separately in experimental conditions, the normal activities of the latter are rarely based on so simple a pattern of behaviour. It is true that the homing honey-bee can orientate itself with regard to the sun and that this is the only mechanism available to the soaring bird as it rises in strange surroundings, but both also make use of other clues in ordinary life as soon as they can appreciate objects in a known environment. In this more elaborate type of orientation two new capacities are added to one or other of the simpler methods—(1) the ability to integrate a number of stimuli simultaneously instead of inhibiting all but one, and (2) the modification of a direct automatic response by the factor of memory through a process of conditioning. By a synthesis of these factors the animal is thus able to deal with a complex situation as a whole (Adlerz, 1903-9 ; v. Buttel-Reepen, 1907 ; Turner, 1908 ; Rabaud, 1924-26 ; Wolf, 1926-27 ; Hertz, 1929-31 ; Friedländer, 1931 ; Tinbergen, 1932-51 ; Tinbergen and Kruyt, 1938 ; Baerends, 1941 ; and others).

In its simplest form this is illustrated by the experiments of van Beusekom (1948) with the homing digger wasp, *Philanthus* (Fig. 50). The initial training situation to which the wasp was conditioned was a square block set at right angles close to the nest and a model of a tree 1 metre from the nest. In the test experiment the block was turned through 45° and the tree displaced first to one side and then the other ; the wasp approached the corner opposite to that

in which the tree was located as if up to the last moment she used both the tree and the block as landmarks.

The pretty experiment of Tinbergen and Kruyt (1938) shows the astonishing rapidity and precision with which the wasp learns to relate its nest to neighbouring landmarks and to appreciate a situation as a whole. A ring of 20 pine-cones was placed around the nest while she was inside ; on leaving she made a study of the locality for 6 seconds only (Fig. 51) ; the pine-cones were then arranged similarly one foot away from the nest ; returning after 90 minutes with a captured bee, she alighted in the middle of the ring of cones, a choice repeated

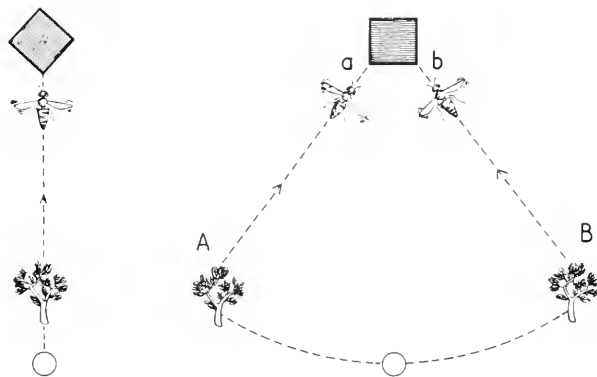


FIG. 50.—THE PATH OF THE DIGGER WASP, *PHILANTHUS TRIANGULUM*.

On the left, the training situation. The path of the wasp (starting from the circle) is directly to its nest at the angle of the block past the tree.

On the right, the test situation. The block is rotated through 45° and the tree moved first to A and then to B. The wasp alights alternately at a and b (simplified from van Beusekom).

13 times, and only found the nest after the original situation had been restored (Fig. 52). A still more extraordinary ability is seen in the wasp, *Ammophila*, which hunts caterpillars too heavy to be brought back on the wing ; as it laboriously drags its prey to the nest it is apparently able, apart from occasional exploratory flights, to utilize the memories of aerial observation, probably aided by light-compass orientation (Thorpe, 1943-56).

Behaviour of this type is obviously determined by the utilization of a number of stimuli and experiment has shown that in making its decision the insect does not condition itself to every available landmark but exercises some degree of choice on principles which would differ from that of a human being. Moreover, the stimuli need not be simultaneous for visual memories may be retained for some considerable time ; thus the bumble-bee, *Bombus*, will fly regularly round a number of fixed landmarks in the same sequence for weeks on end (Frank, 1941). Such studies are of unusual interest but our knowledge of the problems they raise is yet very imperfect ; indeed, experiment has just



Bombus

FIGS. 51 AND 52.—THE REACTIONS OF THE DIGGER WASP.

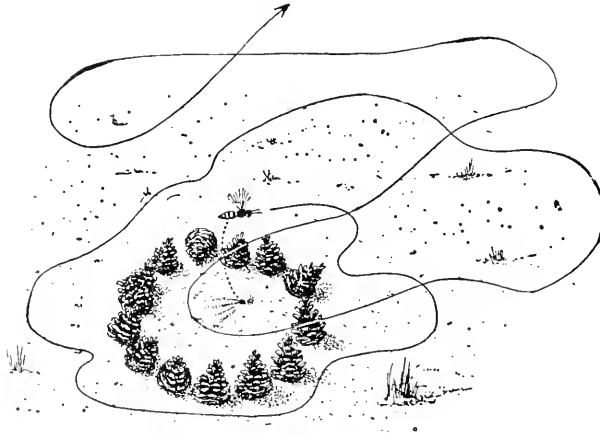


FIG. 51.—The wasp, *Philanthus triangulum*, on leaving the nest in the centre of the ring of pine cones, makes a locality-study lasting 6 seconds and then leaves.

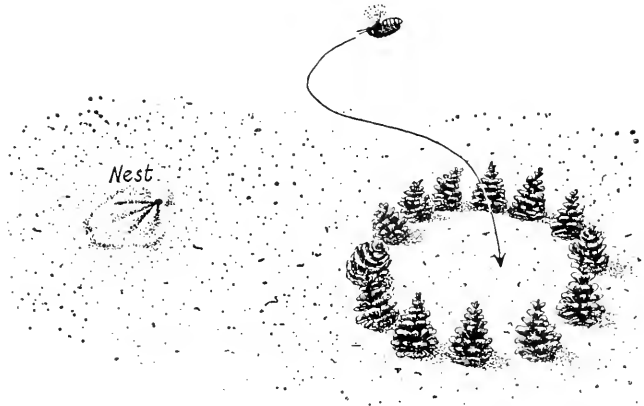


FIG. 52.—The ring of pine cones is then displaced from the nest and on her return the wasp alights in the centre of the ring and will only find the nest after the original situation has been restored (Tinbergen, *Study of Instinct*; Clarendon Press).

begun to elucidate the more complex aspects of animal psychology in which the basic instinctive reactions are modified by experience of the past.

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CHAPTER IV

THE EFFECT OF LIGHT ON PIGMENTATION

THE dramatic effects of light on the pigments of plants and animals have long been recognized. The yellowish-white pallor assumed by plants containing chlorophyll confined in darkness is well known, while the diatoms of the Lakes of Auvergne, equipped with green chlorophyll and brown diatomin, change colour according to the depth of the water in which they find themselves (Héribaud, 1894) ; but the most dramatic effects are evident in the integumentary pigments of *poikilochromic*¹ animals. The spectacular and rapid changes in colour between black and green seen in the chameleon were noted in the fourth century B.C. by Aristotle, while Pliny described somewhat similar changes in the dying mullet. Since classical times a considerable amount of observation and research has been devoted to the subject and a surprisingly wide range of colour changes has been recorded in a large variety of animals—a euglenoid Protozoon, polychaete worms, leeches, Echinoderms, Cephalopods, Crustaceans, Insects, and among Vertebrates, numerous Fishes, Amphibians and Reptiles.²

Biologically these changes may be assumed to serve two purposes, one the antithesis of the other—*cryptic* or protective and *phaneric* or demonstrative. The protective function is the more fundamental and the more common, the demonstrative is a later and more rare acquisition.³

The PROTECTIVE FUNCTION is designed in general to allow the animal to adapt itself to its environment and shows three main modifications. In its most primitive form such a variation in pigment probably developed as a *light-absorptive function* to provide protection against deleterious light and heat ; occasionally pigmentary variations are apparently *thermo-regulatory*—an early attempt at thermostasis—as is seen strikingly in some desert lizards in which colour changes may be induced experimentally by changes in temperature alone (Parker, 1906–38 ; Bauer, 1914 ; Krüger and Kern, 1924 ; and others). The most common and dramatic colour variations, however, have evolved as an *adaptive phenomenon* allowing the animal to become as

¹ ποικίλος, varied ; χρώμα, colour.

² For extensive reviews see van Rynberk (1906), Fuchs (1914), Hogben (1924), Parker (1930–55) and Brown (1950).

³ These are examples of a large group of phenomena termed *allæsthetic* by Huxley (1938) which exert their biological effect through the agency of the distance receptors of another individual—sight, hearing or smell.

inconspicuous as possible and obliterate itself in its environment ; and, as we shall see, this faculty of MIMICRY or HOMOCHROMATISM is sometimes carried to almost unbelievable lengths. particularly among teleostean fishes, the animal not only changing its general appearance in light and shade but assuming the pattern of colour—blue, red, yellow, green, black—of its surroundings (Fig. 53).

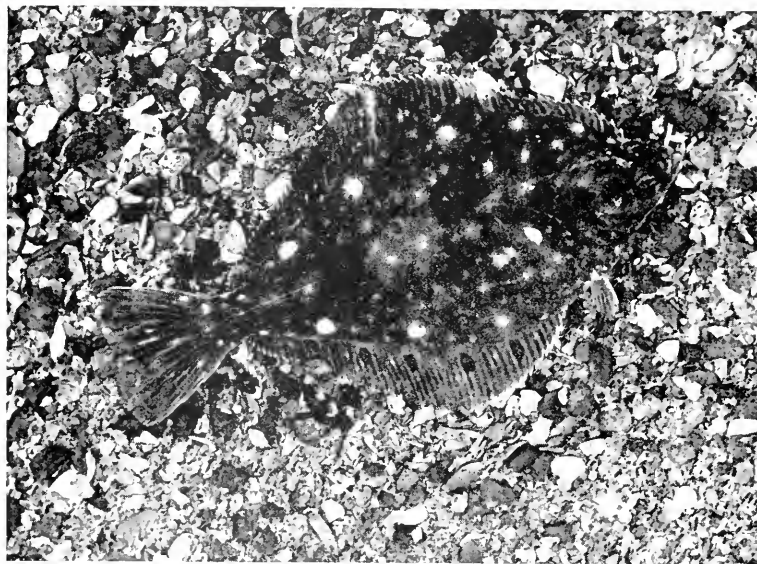


FIG. 53.—THE EUROPEAN PLAICE, *PLEURONECTES PLATESSA*.

Lying in shallow water on the bed of the sea, to harmonize with which it is able to change its colour within wide limits. The camouflage in the figure is obvious (photograph by Douglas P. Wilson).

Occasionally the opposite type of behaviour is apparent and instead of changing its coat to suit its environment, the animal alters its surroundings to suit its own coloration : thus the silvery young of the Malayan spider, *Cyclosa insulana*, normally rests on a silvery silk platform, but as the animal becomes older and brown in colour, it covers the platform with brown debris (Bristowe, 1941). In other cases a suitable environment is deliberately chosen ; thus the desert lark, *Ammomanes*, will settle with great reluctance on a terrain not of its own colouring such as black lava, red earth, or light sand (Meinertzhagen, 1940), just as bark-like moths will adopt postures that make their disrupted wing-design conform with the configuration of the background (Cott, 1940). In still other cases an artificial camouflage is assumed, such as the beetles or dressing-crabs which drape themselves throughout life with a clothing of leaf-fragments, sticks or weeds suitable to each successive environment, or the geometrid larva of Borneo which similarly adorns itself with flower-buds (Shelford, 1902).

DEMONSTRATIVE COLOUR CHANGES, although less common, may also be striking phenomena. These changes in colour whereby the

*Latrodectus**Gasterosteus**Betta**Chlamydosaurus**Bombinator*
in warning
attitude

animal strives to make itself as conspicuous as possible, may be directed towards several ends. In the first place they may serve the essential biological purpose of *reproduction* whereby, simulating the sexual riot of the flowers, colour displays, sometimes of extraordinary vividness, are associated with courtship and mating behaviour, a phenomenon seen in marked degree in certain cephalopods and fishes (Hadley, 1929 ; Parker and Brower, 1935) ; it is a function analogous to the conspicuousness of many male birds adopted possibly for display and distraction in contrast to the cryptic inconspicuousness of the brooding female. It is interesting that such sexual dimorphism is rarely seen in birds which feel secure, either because of their fighting ability or in their colonial habits, the latter finding safety in a flock (Mottram, 1915). In the second place they may be designed for *aggression*, wherein, as if in defiance of all creation, the animal when sufficiently moved to excitement assumes the most blatant hues possible (as in squids, cuttle-fish, teleostean fishes, spiders and lizards : Kleinholz, 1938 ; and others). Less commonly they may have a more social purpose, serving as signals of warning or recognition between members of the same species or as feeding-releasers between parent and offspring (see Marshall, 1936 ; Huxley, 1914-38 ; Cott, 1940-54 ; Armstrong, 1947 ; and others).

Thus when facing an enemy the venomous Australasian spider, *Latrodectus*, turns a fiery red, and the cornered green chamceleon an inky black, opening widely at the same time its brightly coloured mouth. Nowhere, however, in the whole animal kingdom are displays so lavish and theatrical provided as among teleostean fishes in their wild ecstasies of love or fighting ; none so exquisite as the elaborately graceful love-dance of the male European stickleback, *Gasterosteus aculeatus*, when his incandescent blue-green back and transparent red sides glow like neon lighting ; none so awesome as the life-and death war-dance of the ordinarily brownish-grey male Siamese fighting-fish, *Betta pugnax*, as his widespread fins light up in a luminous multi-coloured glory of burning passion which for centuries has whetted the gambling instincts of the Siamese as did cock-fights the English. In these cases the stimulus is purely visual for the stickleback will fight its own image in a mirror with the utmost savagery (Timbergen, 1951).

In other cases a colour-demonstration is made which, strictly speaking, does not involve a true colour change. The Australian frilled lizard, *Chlamydosaurus*, for example, carries around its neck a large frill-like fold supported by cartilaginous rods which can be opened like a huge circular umbrella around the head. When scared the frill is closed and the lizard dashes for safety ; when it turns to face its enemy the great greenish-yellow frill splashed with red forms a striking and terrifying picture in contrast to the saffron yellow of its open mouth, before which the enemy usually retires discomfited. Again, the small European fire-bellied toad, *Bombinator igneus*, has its dark under-surface spotted vividly with yellow or red, associated with a poisonous exudate from the skin ; when danger threatens the animal throws itself on its back or arches its body to proclaim its unsuitability as food.

The mechanism of the colour change varies in different species. In the simplest unicellular form, *Euglena*, a red hæmatochrome pigment migrates from a deeper position beneath the green chloroplasts to disperse itself superficially under the influence of light (Johnson, 1939); but the most common mechanism is through the activity of special integumentary cells¹ called CHROMATOPHORES (χρωμαζ, colour; φόρος, a carrier). Occasionally the phenomenon is morphological involving a change in the number of functioning chromatophores or an alteration in the quantity of pigment in each. This, a relatively slow mechanism, is well exemplified in the pigmentation that can be induced in the white belly of flounders if normal fish are kept in a black tank or are blinded and are illuminated from below (Osborn, 1940). Sometimes, as in certain insect larvæ and spiders, this is the sole mechanism of colour-change available (Gabritschevsky, 1927); it is usually less obvious and impressive than the more common method which is responsible for the dramatically vivid colour changes in poikilochromic Crustaceans, Fishes, Reptiles and Amphibians.² This—a functional or physiological change—involves merely a redistribution of pigment. The change may be effected by a single pigment which at one time is concentrated into tiny spots lost in a pallid background of skin so that it contributes little to the colour of the animal, at another, dispersed so that the animal becomes appropriately tinted. Alternatively a pigment of one colour may stream in front of or retire behind pigments of other colours so that surprising changes of hue may rapidly occur. The two methods, morphological or physiological, are not mutually exclusive, for if the conditions determining the second are maintained for a sufficiently long time, permanent morphological changes tend to occur, a generalization sometimes known as Babák's law (1913).

*Euglena*

Warm-blooded animals, on the other hand, can only change their colour by the slow and laborious process of renewing their inert feathers or hairs; to this there are a few exceptions wherein specific stratagems are adopted, such as the antelope-jackrabbit which turns white in its flight by rolling up the skin of its belly on the side towards its pursuer.

Two major types of chromatophores occur. In Molluscs (cuttlefish and their allies, squid, octopus), the chromatophores are in highly organized groups of cells in which the pigment is redistributed by neuromuscular activity. Each organ consists of a central cell filled with pigment (red, brown or yellow) around which radiate a number of muscle-fibres which, on their simultaneous contraction, pull out the



Cuttlefish

¹ In certain transparent Fishes part or all of the colour pattern is found in internal organs such as the peritoneum and meninges.

² Crustaceans, Keeble and Gamble (1903-5); various Vertebrates, Babák (1913), Brown (1934); Fishes, Odionne (1933); Amphibians, Sumner (1935).

small pigmented cell-body into a great disc some twenty times the diameter of the original sphere ; a nerve-fibre supplies each muscular cell and the resulting changes are rapid (Figs. 54 and 55).¹ In all other animals the chromatophores are single cells ; usually they are specialized cells provided with arborizing processes, arranged singly or in a syncytium, and by a process of cytoplasmic streaming the pigment may be concentrated into inconspicuous punctate masses in the centre of the cell or dispersed throughout the branching structure to give a diffuse colour to the animal (Figs. 56 to 59).² In Insects, however, the ordinary epidermal cells fulfil this function ; normally a dark brown-black pigment lies beneath an evenly disposed yellow-green pigmented

FIGS. 54 AND 55.—A CHROMATOPHORE OF THE CEPHALOPOD.

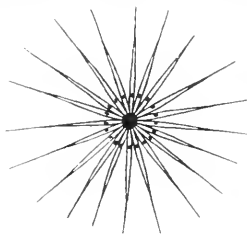


FIG. 54.

FIG. 54.—The appearance of the chromatophore with the radiating muscular cells and the small concentrated clump of central pigment.

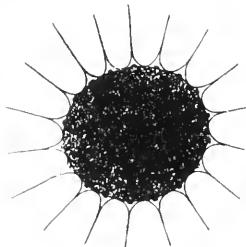


FIG. 55.

FIG. 55.—The extended mass of pigment pulled out by contraction of the muscle cells (after Bozler).

layer, and on stimulation the former migrates to the surface and disperses itself over the lighter layer thus darkening the animal (Figs. 60 and 61) (Giersberg, 1928-30).

The coloration resulting from the migration of pigment is often assisted by its new relationship to static pigment. Under the chromatophores of Cephalopods and Crustaceans, for example, there is an immobile layer of light-reflecting pigment so that considerable variations in colour are possible depending on the amount of light permitted to pass to the deeper tissues (Webb *et al.*, 1952). In Insects, as we have seen, the variegation is enhanced by the migratory brown or red pigment covering over or retreating behind the static green and yellow pigments. In Amphibians such as the tree-frog, *Hyla arborea*, a colour change from green through lemon-yellow to grey is attained by variation in the dispersion of melanin underneath layers of yellow and white



Hyla arborea

¹ See especially—Phisalix (1894), Hertel (1907), Hofmann (1907-10), Fröhlich (1910), Bozler (1928).

² See especially—Spaeth (1913), Perkins (1928), Matthews (1931), Perkins and Snook (1932), Brown (1935), and others.



FIG. 56. —THREE STAGES IN THE DISPERSION OF PIGMENT IN A MELANOPHORE OF THE LIZARD, *TARENTOLA* (Hogben).

FIGS. 57 TO 59.—PIGMENT SPOTS IN WEB OF A FROG IN DIFFERENT CONDITIONS (Hogben).

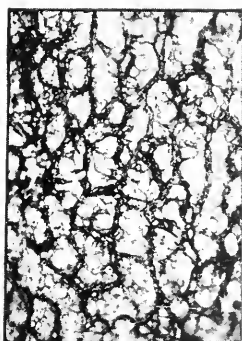


FIG. 57.—Dark animal.

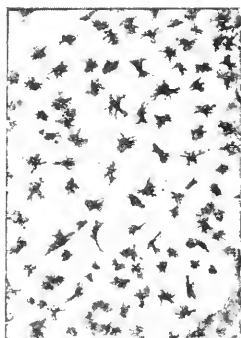


FIG. 58.—Intermediate condition.

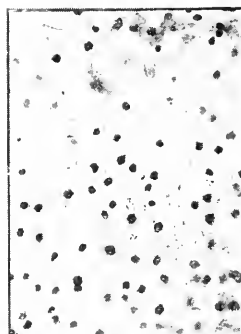


FIG. 59.—Pale animal.

cells and its streaming towards the surface between them (Schmidt, 1920). A comparable arrangement may be seen in Reptiles ; thus in the lizard, *Anolis*, the animal is darkened by the streaming of melanin in the processes of chromatophores to become superficial to an inert whitish layer (v. Geldern, 1921 ; Kleinholz, 1938) (Figs. 62-3), while the proverbial chameleon changes from a dark brown to a light green depending on the degree of dispersion of the melanin which lies in front of a sheet of four different kinds of colour-cells.

The types of pigment also vary, but the intimate chemical nature of many is unknown. The most primitive and universal pigment is melanin¹ of a dark brown colour ; the cells containing it are usually monochromatic and are termed *melanophores*. A second type of pigment—more vivid and varied than the dull brown of melanin—is



Anolis



Chameleon

¹ For a discussion of the chemical nature of melanin, see p. 118.

FIGS. 60 AND 61.—THE PIGMENTARY CHANGES IN THE STICK-INSECT, *DIXIPPUS*.

There are 3 types of pigmentation : (A) the cross-hatching indicates a static layer of yellow-green pigment underneath the cuticle, (B) the fine dots indicate red pigment which may be either aggregated into clumps or dispersed, and (C) coarse dots indicating brown-black pigment which migrates from a deep site underneath the nuclei to a superficial position underneath the cuticle (after Giersberg).

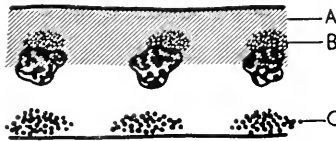


FIG. 60.—The epidermis in the light-adapted stage.



FIG. 61.—The epidermis in the dark-adapted stage.

comprised of various fat-soluble carotenoids¹ contained in *lipophores*. In Invertebrates (Crustaceans, Insects) the chromatophores are frequently polychromatic since each may contain a variety of these pigments—blue-green, orange, yellow and red—sometimes each with a separate distribution within the cells.² In Vertebrates the chromatophores are usually monochromatic—red (within *erythrophores*), yellow (within *xanthophores*) or green³—one animal often having several types of pigment in different integumentary cells (purple astacene and yellow lutein in the brown trout, *Salmo trutta*, Steven, 1948). A third pigmentary factor is found extensively both in Invertebrates and Vertebrates

*Salmo trutta*

FIGS. 62 AND 63.—COLOUR CHANGES IN THE LIZARD.

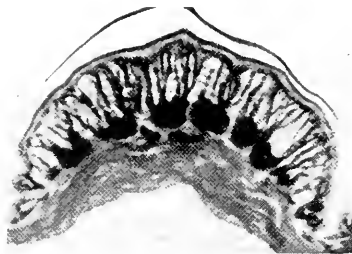


FIG. 62.—The deposition of the melanophores in the brown state when the branches of these cells extend into the stratum germinativum.

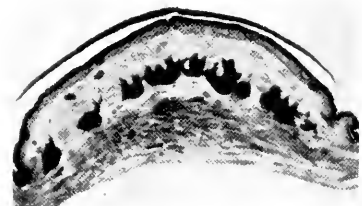


FIG. 63.—The lizard in the green condition when the pigment is concentrated beneath the static pigment in the superficial layers.

The stratum corneum has been displaced from the section (Kleinholz).

¹ The carotenoid pigments are of wide distribution and great biological interest, playing a part as sensitizers to the phototropic movements of plants, the phototactic movements of animals, and also participating in visual processes. Their nature will be discussed at a later stage (p. 118).

² In Crustaceans—Kühn and Lederer (1933), Fabre and Lederer (1934); in Insects—Schleip (1910–15), Giersberg (1928).

³ See Fox (1947).

—guanine. This may form a white highly reflecting layer, as in Crustaceans, or, as in many Vertebrates, may be contained in white *guanophores* or variegated *iridocytes*, the iridescent colour changes of which are due to the arrangement, form and movements of plate-like crystals of guanine—a form of coloration akin to that due to the diffraction of light by the scales of fish and reptiles or the feathers of birds. The colour changes in these cells are sometimes quite remarkable; thus in the killifish, *Fundulus*, a single iridocyte may exhibit blue-green, orange, yellow and red phases in successive moments.

*Fundulus*

The factors causing colour changes in animals include extremes of temperature, humidity, contact stimulation, and psychic stimuli, particularly excitement and fear; but the most general and much the most important is light.

Light acts upon chromatophores in one of three ways—by a direct, primary effect on the cells themselves, by a secondary reaction through the eye, or by indirect reactions through receptor mechanisms other than the eyes (the central nervous system and the pineal body).

A further response—the endogenous *diurnal variation* in coloration, largely controlled by hormones and nervous centres situated in the mid-brain—we have already discussed.¹

(a) When light acts directly upon the chromatophores themselves the reaction may be called a PRIMARY RESPONSE. This is the most primitive mechanism and the only one available to unicellular plants (diatoms) or animals (*Euglena*), but it is frequently retained in higher forms, usually as a generalized darkening in the shade and lightening with illumination, a change, however, normally obscured by the more dominant secondary responses through the eyes. The primary response, however, can be observed in young specimens the chromatophores of which have not yet come under the control of the secondary mechanism, in blinded animals (Osborn, 1940), in denervated regions after nerve section and degeneration, and in isolated fragments of the skin when exposed to illumination, a reaction demonstrated in crustaceans (Keeble and Gamble, 1905) and in some sea-urchins (Kleinholz, 1938; Millott, 1954–57) (Figs. 64 to 67).



Diatom

The direct motor response of individual ectodermal cells to the stimulus of light survives among the higher animals in the movements of the retinal rods and cones² and in the contraction of the pupillary muscles, both of which are ectodermal in origin. In the iris of Cephalopods, Fishes and Amphibia a direct contraction to light commonly occurs,³ and although the primitive response in the higher Mammals and man has been replaced by a reflex neuro-mechanism,

¹ p. 19.² p. 731.

³ Brown-Séquard (1847–59), Budge (1855), Müller (1860), Schur (1868), Steinach (1890–92), Magnus (1899), Guth (1901), Marengi (1902), Hertel (1907), Young (1933), Weale (1956), and others.

FIGS. 64 TO 67.—PIGMENTARY CHANGES WITH LIGHT INTENSITY
IN A SEA-URCHIN.

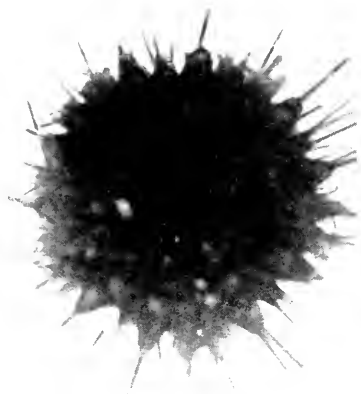


FIG. 64.

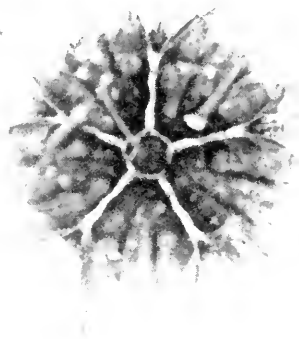


FIG. 65.

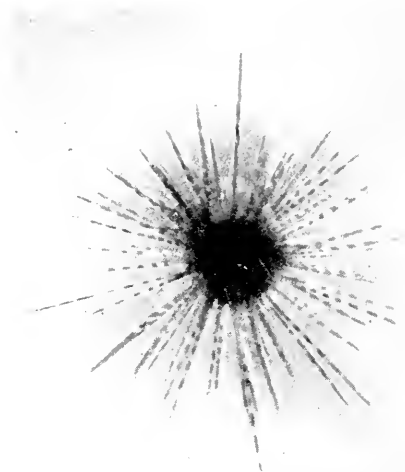


FIG. 66.

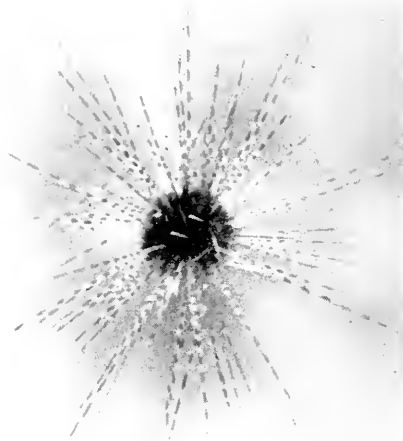


FIG. 67.

To show the variation of pigmentation in a young specimen of *Diadema antillarum*. In the light-adapted phase the animal appears uniformly black owing to the dispersion of melanin pigment (Fig. 64). In the dark-adapted phase the melanin recedes from the aboral surface leaving beautifully defined patterns of white lines and a ring, an effect due to the concentration of pigment (Fig. 65).

In older specimens, the changes are less marked (Figs. 66 and 67) (N. Millott).

it may still be elicited with the more effective stimulus of ultra-violet light after all connections with the central nervous system have been severed.

(b) The most dramatic reactions follow stimulation of the eyes (SECONDARY RESPONSES). Hogben and Slome (1931), for example, found that in the case of the clawed toad, *Xenopus*, when the field of vision was occupied by a light-scattering surface the animal became pale, when set in the dark background of a light-absorbing surface the animal suffered generalized darkening of the skin, a response abolished on removal of the eyes. While the primary responses react in general to the total intensity of light, the secondary response is usually based on the ratio of the amount of *incident* light entering the eye directly from above to the amount of *reflected* light from the background, so that on a dark background, when the ratio is large, the animal becomes dark and on a light background, when the ratio is small, it becomes pale; it is to be noted that these changes occur without regard to the intensity of the total illumination (Sumner, 1911-40; Sumner and Keys, 1929; Brown, 1936; Sumner and Doudoroff, 1937). This influence of the reflectance or *albedo* of the background (to borrow an astronomical term) has been fully established by experiment; thus the effect of a dark background can be faithfully reproduced by making the lower half of the cornea opaque¹; reversal of the fish or of the illumination or the background produces the expected effect; and Butcher (1938), on rotating the eye of the killifish, *Fundulus*, through 180°, found that it gave its tawny response to a yellow background only when the latter was above the animal.

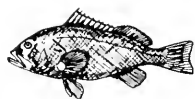
In his work on teleostean fishes Sumner (1940) established that the reflectance of the substrate had an important effect on morphological colour changes also, for he found that the melanophore count and the total quantity of melanin varied inversely as the logarithm of the reflected light. The mathematical nature of the relationship is interesting and unexpected; it recalls Fechner's modification of Weber's Law defining the relationship between the intensity of stimuli and their sensory appreciation, and suggests that in assuming control of these colour changes the eye applies the same quantitative standards as govern its sensory activities.

In addition to this general quantitative reaction, a differentiated response to the spectral nature of the light reflected from the background is relatively common so that the animal can assume the colour of its environment, sometimes with remarkable rapidity and accuracy. This apparently extraordinary reaction was first scientifically described in the chameleon prawn, *Hippolyte*, by Keeble and Gamble (1899) and many instances have now received study. The prawn, *Palæmon*, for example, can manipulate its red, yellow and blue pigments, so that with-



Hippolyte

¹ In the insect, *Dirippus*—Atzler (1930); Priebatsch (1933); in shrimps—Hanström (1937-38); in fishes—Sumner (1940).

*Epinephelus**Triturus cristatus**Phoxinus*Ammocete larva
of lamprey

in a few days it can adapt itself to its habitat by becoming red, yellow blue, green, white or black (Brown, 1935), a facility possessed in some degree by several crabs¹ and Cephalopods.² Such a change may occur rapidly; thus the larvæ of butterflies (Brecher, 1922) and salamanders (Kammerer, 1920) when placed under variously coloured glasses readily change their hue; and not only the tone of the general background but its colour-pattern may be simulated with great fidelity by certain teleostean fishes. The most remarkable changes of this type are seen in the groupers (*Epinephelus*) that swim over the variegated patterns of the coral reefs in tropical waters and within a few minutes may change a livery of bright blues and browns into an equally brilliant costume of yellow and black; a similar virtuosity is seen in flat-fishes such as the flounder, *Paralichthys albiguttus* (Kuntz, 1916; Mast, 1916). It is interesting that adaptation during the early stages of development may play an important part in determining the final pattern of colour in the adult; thus if the larvæ of the crested newt, *Triturus cristatus*, develop on a dark background the yellow markings of the adult become suppressed, if on a light background, the dark markings suffer a similar fate (Lautz, 1953). It is to be noted that all these reactions are completely dependent on the eyes and have invariably been shown to be lost if the animal is blinded or even if it is dazzled by a blinding light which abolishes the contrast between the dorsal and ventral portions of the retina (octopus, Prince, 1949).

(c) Occasionally INDIRECT RESPONSES may follow stimulation of receptor mechanisms other than the eyes—the MID-BRAIN as in some fishes (*Phoxinus*—Scharrer, 1928) or the PINEAL BODY as in lampern larvæ (Young, 1935) or teleostean fishes (Breder and Rasquin, 1950).

The central organization of these pigmentary changes is as varied and complex as the variations in the colours themselves, and in view of the multiplicity of the types of chromatophores and their reactions it is not surprising that our knowledge of their control is by no means complete in spite of much research. Apart from local primary reactions, two methods of coordination are found, hormonal and nervous, the first the more primitive and slower in its development, the second the more elaborate and efficient. Sometimes the one is present alone, as is seen, on the one hand, in the simple hormonal control found in Crustaceans, the more primitive Fishes, frogs and lizards, or, on the other hand, in the simple nervous control found in the leech or the chameleon. More often the two are combined in a dual mechanism of coordination, the hormonal control being sometimes the preponderating influence as in Insects or the eel, but usually being

¹ *Portunus*—Abramowitz (1935); *Planes*—Hitchcock (1941).

² *Sepia*—Kühn and Heberdey (1929), Kühn (1950).

dominated by the nervous mechanism as in Cephalopods such as the octopus or the more highly developed Teleosteans such as the catfish. The hormones (*chromatophorotropins*), of which there may be more than one with mutually antagonistic reactions, are elaborated in Crustaceans in the neuro-secretory cells formed in the eye-stalks and elsewhere in the central nervous system¹; in Vertebrates the pituitary-hypothalamic complex² is the primary source although the adrenals may provide an antagonistic element. The nerve supply may be simple with one type of fibre which is pigment-concentrating as in the dogfish or the chameleon, or it may be dual comprised of two opposing types of fibre, one resembling adrenalin with a pigment-concentrating (sympathetic) action being antagonized by a second resembling acetylcholine with a pigment-dispersing (parasympathetic) effect.

Among ANNELIDS, such as some polychaete worms (Hempelmann, 1939) and leeches (Wells, 1932; Janzen, 1932; Smith, 1942), most of which become pale in darkness and dark when illuminated, the evidence suggests that the control is primarily nervous, correlated most effectively through the ocelli at the anterior end but operated less efficiently by widely distributed photoreceptors through segmental reflexes. Thus if a leech is decapitated or stimulated faradically, a pale animal kept in darkness will become pigmented, but if the nerve-cord is truncated the change passes only to the level of trans-section; while decapitated animals show the same responses as normal animals but respond more sluggishly (Smith, 1942). Among these animals there is no evidence of a response to the background.

In CEPHALOPODS there is a slowly acting hormonal control, probably mediated by substances of the nature of tyramine and betaine; the former has an adrenalin-like action increasing the tonus of motor centres and producing a dark coloration, while the latter, like acetylcholine, decreases the tone of the chromatophores and lightens the animal. The injection of these substances produces the same colour changes as also does the transference of blood from a dark to a light animal (Sereni, 1928-30). This simple and fundamental chemical action, however, is dominated by nervous activity; the stimulus is received primarily through the eyes, control being maintained through centres in the cerebral and suboesophageal ganglia, the isolation of which by nerve section stops all colour change in the area affected, and the response is effected probably by a double innervation, both excitatory and inhibitory, to the muscles of the chromatophores (Phisalix, 1892-94; Sereni, 1927-28; Bozler, 1928-29).

Among INSECTS the control is both hormonal and nervous and the part played by the eyes varies. In this respect the stick-insect, *Dixippus*, has been investigated most extensively (Giersberg, 1928).



Leech

Cephalopod
(Octopus)*Dixippus*¹ p. 552.² p. 556.



Grasshopper

In it, the eyes are the sole photoreceptors and their occlusion or section of the optic tracts inhibits all normal responses (Atzler, 1930); but the fundamental role of hormonal control is seen in the fact that transplanted portions of integument react normally long before nervous connection can be established (Janda, 1936). On the other hand, in the grasshopper, *Acrida turrita*, some colour changes (adaptation to red, orange, yellow and violet) are said to occur after the eyes are totally varnished, while a green colour can be developed only if the eyes are functioning (Ergene, 1952).

Among CRUSTACEANS the vividly dramatic colour changes are



FIG. 68.—COLOUR CHANGES IN CRUSTACEANS.

The three shrimps (*Crago*) were initially coloured alike, as the specimen on the left. This was used as a control and showed no change after an injection of sea-water. That in the centre was injected with an alcohol-insoluble fraction of the commissures; that on the right by a total water-soluble fraction of the commissures (Brown and Klotz).



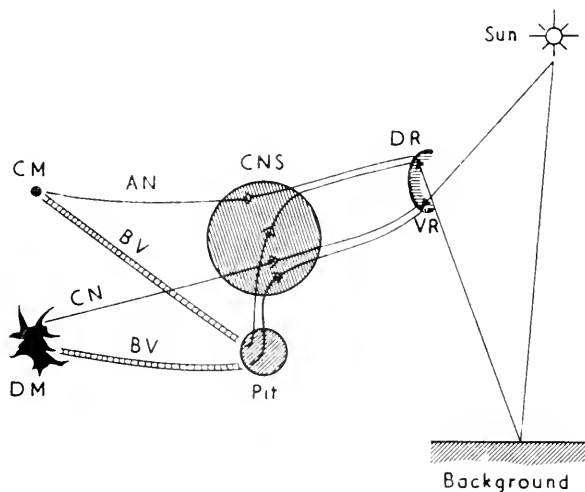
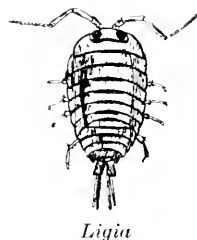
Prawn

entirely mediated by hormones elaborated in the cephalic neuro-secretory system.¹ That a blood-borne agent was the responsible factor was first demonstrated by Koller (1925-30) who found that the colour of a lightly coloured shrimp, *Crago vulgaris*, could be altered by blood transfusion from a darkened specimen. Perkins (1928-32) thereafter discovered in the prawn, *Palaeomonetes*, that denervation of a region had no effect on colour responses while occlusion of the blood supply inhibited them; he also demonstrated that injection of an extract of the sinus gland induced blanching in a blinded animal while removal of the eye-stalks resulted in the assumption of a permanently darkened appearance. These early results have been amply confirmed and it would appear that the intricate control of the chromatophores of Crustaceans is effected by at least two and sometimes three or four

¹ See further p. 554.

chromatophorotropins antagonizing and supplementing each other, neither species- nor genus-specific, secreted in various parts of the neuro-secretory system¹ (Fig. 68). In some cases the process is more complex and adaptation to the background is achieved by the production of different hormones when the dorsal or the ventral aspect of the retina is stimulated (the Isopod, *Ligia oceanica*—Smith, 1938).

In CYCLOSTOMES and the more primitive fishes such as the SELACHIANS² hormones derived from the pituitary seem to be the only active agents in the control of the chromatophores, a pigment-



*Anguilla*

1935 ; Hogben, 1936). In TELEOSTEAN FISHES, however, which show more elaborate colour changes than any other species, a dual mechanism emerges for a more efficient nervous control has developed, depending on the excitability of specialized retinal areas above and below the level of the optic nerve (Hogben and Landgrebe, 1940) (Fig. 69). In some types, it is true, the hormonal influence remains preponderant ; this is seen in the eel, *Anguilla* (Neill, 1940 ; Waring, 1940), or in the minnow,

FIG. 70.—COLOUR CHANGES IN THE FEMALE GUPPY, *LEBISTES RETICULATUS*

On the left the normal animal ; on the right a fish after 25 μ g. per ml. of LSD (D-lysergic diethylamide) had been added to the water of the aquarium (Sandoz *J. Med. Sci.*, 1956).

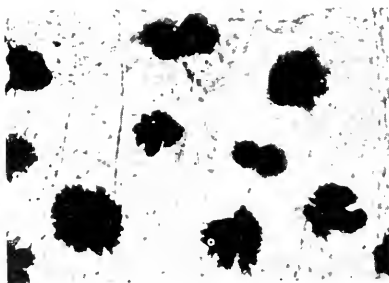
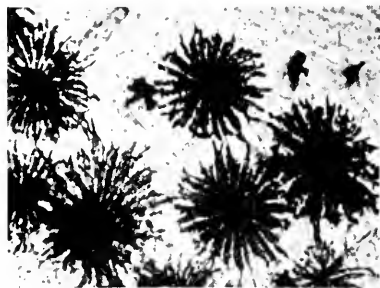
FIGS. 71 AND 72.—THE MELANOPHORES OF THE GUPPY, *LEBISTES RETICULATUS* (Sandoz *J. Med. Sci.*, 1956).

FIG. 71.—After adaptation to a light environment.

FIG. 72.—After LSD (25 μ g. per ml.) had been added to the water of the aquarium.

Phoxinus phoxinus, in which even section of the spinal cord fails to alter the response to the background (Healey, 1951-54 ; Gray, 1956). In most Teleosteans, however, colour changes are dominated by a nervous control which persists in hypophysectomized animals. That the changes in the chromatophores were determined by chemical mediators liberated at the nerve terminals has been shown in a striking series of experiments by Parker (1940-55), who studied the effects of sectioning the radial nerves of the tail-fin. The chromatophores of Selachians possess a single innervation mediated by an adrenalin-like substance, selachine, which is pigment-concentrating (the dogfishes, *Mustelus* and

*Mustelus*

Squalus—Parker, 1935–36); Teleosts possess a double innervation with, in addition, pigment-dispersing fibres the action of which is mediated by acetylcholine (the killifish, *Fundulus*—Parker, 1934; the catfish, *Ameiurus*—Mills, 1932, Parker, 1940–41; and other species). These two types of nerve correspond to the sympathetic and parasympathetic systems of warm-blooded animals since adrenalin blanches and acetylcholine darkens the eserinizated animal (Giersberg, 1930; Smith, 1931). Similarly, darkening of certain Teleosts (the guppy, *Lebistes reticulatus*) can be brought about by adding D-lysergic acid diethylamide to the water of the aquarium (Cerletti and Berde, 1955) (Figs. 70 to 72). At the same time, however, even in these

*Squalus**Ameiurus*

FIG. 73.—THE EFFECT OF THE INJECTION OF PITUITRIN ON A FROG.

The right animal injected six hours previously with pituitary extract from a fetal ox; left, control (Hogben).

fishes some hormonal influence remains since pituitary extracts are slowly effective in denervated areas (Matthews, 1933; Kleinholz, 1935; Abramowitz, 1937).

AMPHIBIANS were the first class of animals in which a humoral control of colour was demonstrated, when P. E. Smith (1916) showed that hypophysectomized tadpoles remain indefinitely pale. Although there is some evidence of a minor nervous influence in some species such as the darkening of the leg of the toad, *Bufo arenarum*, on section of the sciatic nerve and its blanching on peripheral stimulation of the cut nerve (Stoppani, 1942), it may be said in general that amphibian chromatophores are essentially under humoral control. This is maintained by two antagonistic hormones elaborated in the pituitary-hypothalamic system—a melanin-concentrating *W*-substance causing

*Bufo*

*Rana**Xenopus**Anolis**Phrynosoma*

blanching, mediated by the pars tuberalis, and a melanin-dispersing *B-substance* (intermedin) mediated by the posterior or intermediate lobe; their relative concentration in the blood is determined by environmental stimuli operating through the eyes and their activity is usually abolished when these or the optic nerves are destroyed, although some residual responses remain after removal of both eyes which may be due to the direct action of light on the hypothalamic region (Rowlands, 1952-54). These conclusions have been confirmed by the effects of excision of the whole or parts of the pituitary and by the induction of colour changes by the injection of extracts of the gland both in the frog, *Rana*,¹ and in the African clawed toad, *Xenopus laevis*² (Fig. 73). It is also interesting that injection of pineal extract produces a contraction of the melanophores of *Xenopus* (Bors and Ralston, 1951) while pigmentary changes are constantly produced in tadpoles by feeding on pineal tissue (McCord and Allen, 1917).

REPTILES, like Amphibians, show less elaborate responses to light than teleostean Fishes; the only conspicuous changes occur among lizards and the only active cells are the melanophores which send up pigment into their branches entwined among the variegated chromatophores, thus varying the colour scheme; the gaiety of their various costumes is due to individual variation in these static cells. The only phôtic response is to light entering the eye, and the colour of the background is without primary significance. Within these limitations, however, the large family of lizards shows every possible variation in control. On the one hand, the iguanid, *Anolis* (the "Florida chameleon"), shows little evidence of nervous intervention; it becomes dark brown in bright illumination, pale green in darkness; a hypophysectomized or a blinded animal becomes light green and thereafter loses all colour responses except a peculiar mottling on electrical stimulation or on the injection of adrenalin; while denervated areas of the skin respond as do normal areas (Kleinholz, 1938) (Figs. 62 and 63). An intermediate position is occupied by such iguanids as the American horned "toad," *Phrynosoma*. The chromatophores of this animal are under the influence of pigment-concentrating nerve fibres and react to adrenalin; stimulation or section of these fibres results respectively in blanching or abolition of responses. At the same time the injection of pituitrin or of the blood of a darkened specimen induces darkening, while hypophysectomy or the injection of adrenalin, adrenal extract or of blood from a pale animal induces blanching (Redfield, 1918; Parker, 1938). It would seem that the two antagonistic hormones act directly on the chromatophores since they are

¹ Hogben and Winton (1922-23), Steggerda and Soderwall (1939), Parker and Scatterry (1937).

² Hogben and Slome (1931-36), Atwell and Holley (1936).

equally effective in areas denervated by nerve section. On the other hand, in the chameleon the chromatophores show no evidence of hormonal control and appear, apart from the primary response characteristic of this animal, to be influenced solely by one set of pigment-concentrating nerves; denervation results in darkening, possibly due to the absence of tonic impulses, whereafter there is a complete absence of further responses (Hogben and Mirvish, 1928; Zoond and Eyre, 1934; Sand, 1935).

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CHAPTER V

THE EMERGENCE OF VISION

IN the varying reactions of living organisms to light that we have now studied, in some cases vision does not—or need not—co-exist, in others an associated sensory impression is conjectural and unimportant while in others it seems to be a necessary accompaniment ; indeed, it is no easy matter to decide where its origin lay or when the sense of vision first became a factor in conscious behaviour. There are many creatures which have no eyes (as we understand the term) and yet “ see ” (using the word in its widest sense) ; and equally reasonably it may be said that there are many which have what we may well call “ eyes ” and yet see not.

To a considerable extent the matter is one of definition ; on the one hand, few would acquiesce with Max Schultze (1868) who spoke of the transformation of luminous into nervous energy as vision ; more would agree with Hesse (1908) who contended that the *light-sensitiveness* of primitive creatures did not imply the possession of a *light sense*. On the other hand, there are those who would ascribe to all animals which react to light a sentiency, no matter how vague (McDougall, 1933). To many this may seem gratuitously anthropocentric ; for if such an awareness, tinged with affective tone, is ascribed to the amoeba as it flees from a bright light and expands in mid-intensities of illumination, is it to be ascribed also to the speedwell which opens its petals to the mid-morning sun? The question is disputable ; but whichever attitude we adopt the most illegitimate premise from which we can reason is the assumption that an organism has the same appreciation of light and patterns of shade or hue as ourselves, whether it reacts diffusely without specific end-organs or whether it is possessed of eyes more highly differentiated for the resolution of visual images than the relatively simple eyes of man.¹

It must be remembered, however, that vision is one of the latest senses to be evolved and that in its phylogenetic development it lingered long behind those depending on mechano-receptors and chemo-receptors. Even when a considerable stage of complexity had been reached there was little attempt at discrimination ; for this purpose reliance was placed upon those senses which are more fully developed in primitive life—the tactile sense, the chemical sense, and the olfactory sense. The great majority of animals are non-visual

¹ The few sign-stimuli to which the vision even of birds is limited are striking examples (p. 66).

creatures depending essentially in their behaviour on non-visual stimuli.

For example, the scallop has numerous visual cells around the edge of its mantle, and if these are stimulated by the "sight" of its enemy, the starfish, no response except the awareness of the presence of something is elicited, and no attempt at flight is made; but whenever some extract of starfish is added to the water in which the animal lies, the scallop immediately runs away (Dakin, 1909; von Uexküll, 1921). Moreover, in *Pecten*, no response is called forth until the object moves, and any movement of any object excites the same response, a protrusion of the tentacles; these are endowed with organs of



FIG. 74.—THE SENSORY REACTIONS OF THE WATER BEETLE.

A watery meat extract is contained in the bag. The feeding responses of *Dytiscus marginalis* show its dependence on chemical stimuli rather than visual (Tinbergen, *Study of Instinct*; Clarendon Press).

chemical and tactile sensitivity which explore the object "intelligently", and on the results of their findings the animal either eats or flees (Dakin, 1910). The purpose of this response is obviously to secure further information in a form in which it is analysable. Even in man the olfactory sense organs are relatively more fully developed than the visual at birth; a fish with its olfactory nerves severed ceases to feed spontaneously (Steiner, 1888); and the lately-born rabbit will die of starvation if deprived of the sense of smell because it cannot find the teats of its mother, even although it has been allowed to make use of its eyes before it has suffered the loss of the more fundamental sense.

It must also be remembered that even although vision is well developed it may not be used in many innate reactions for the efficient execution of which it would appear to us to be of value. The feeding response of the carnivorous water-beetle, *Dytiscus marginalis*, is a good example of this (Tinbergen, 1936) (Fig. 74). This beetle has elaborately developed compound eyes and can be trained to respond to visual stimuli. Its feeding response, however, is released only by chemical and tactile stimuli, and visual impressions, even those of a moving prey, never release this reaction. Thus in the presence of a watery meat extract it neglects the source but, going to the region of highest concentration, it attacks any solid object it touches.

Of the three fundamental effects of light on living organisms—the stimulation (or occasionally the depression) of metabolic activity, the orientation of movement, and the control of pigment and colour—it would be reasonable to assume that the first, equally shared between plants and animals, does not necessarily involve vision as a conscious experience, occurring as it does in Protozoa and eyeless types.¹ In its more primitive form this activity may conjecturally be accompanied by a vague sentiency, but this can be little more than an awareness of light, and even in its most advanced forms it is essentially a chemical or hormonal function for the implementation of which eyes are effective but not unique receptors. The last—the control of colour—is a late evolutionary development, and although poikilochromic reactions would appear to occur without conscious accompaniment, in their higher developments they would seem to imply the existence of a visual sense in the organism for whose benefit (or confusion) they are intended. The economy would seem unnatural and contrary to all biological trends that at one time urged all plants except the modest Cryptogams, in their struggle for existence in a cooling world, to luxuriate so shamelessly in the blatant sexual exhibitionism of flowering if the pollinating insects could not both see and appreciate their charms; their appreciation, however, has probably no resemblance to the interpretation of the same imagery by the human brain. Equally uneconomic would be the scandalously attractive dress put on by many fishes and birds for their love-making. Clearly, if they are endowed with biological usefulness and survival-values, allæsthetic characters—and without these endowments they would not persist—must be appreciated by other organisms.

Although the eyes serve as the receptors for many adaptive colour changes, this function need not imply that the animal itself has any conscious appreciation excited by shifting visual patterns. Even when the responses are mediated nervously and are rapid and complex, as in teleostean fishes, they show no parallelism with what is known of the visual functions of the animals concerned, for reflex alterations of the chromatophores may occur to suit differences in shade of the back-

¹ Such, for example, as the white cave crayfish, *Cambarus ayersii* (Wells, 1952).

ground too small to excite visual discrimination in training experiments. Many of the reactions, as we have seen, are hormonal ; some may occur in eyeless animals ; and indeed, in species wherein these organs are necessary for their occurrence the chromatophores may still respond if the eyes are transplanted to a new location in the body (as was demonstrated in the adult fish, *Fitzroya lineata*, by Szepsenwol, 1938). Temperature and humidity, as seen in Amphibians and Reptiles, may be equally or more effective stimulants in comparison with light, and although heat and light usually coincide in natural surroundings, the paling of the desert lizard in the heat of noon so that it blends with the sand is fortuitous so far as its own vision is concerned. Tactile organs are sometimes adequate receptors as is seen in the control of chromatophores by the suckers of Cephalopods (Steinach, 1901) ; while the adoption of a brown colour by the European tree-frog, *Hyla arborea*, when it steps on a rough surface and of a green colour on a smooth surface brings about an environmental adaptation to a background of tree-bark or leaves respectively as adequate as any photic response. Indeed, many of these colour reactions are fortuitous so far as adaptation to a background is concerned ; thus the iguanid lizard, *Anolis*, turns green in the shade and brown when exposed to light, and it is merely coincidental that in its natural haunts it usually becomes invisible on a background of shady foliage in the first event or of soil in the second, since, if it is removed from the shade upon a green leaf and placed in the sun still sitting on the leaf, it promptly changes its colour into a vividly contrasting brown (Wilson, 1939).

It is essentially from the primitive motor response to light that vision almost certainly developed. In natural circumstances these tropisms and taxes are invariably of biological utility, and it would appear that *the essential and primary function of vision was the control of movement in order to attain an optimum environment as efficiently as possible*, a function which is eventually employed for the avoidance of obstacles, the pursuit of prey and flight from enemies, and survives in man in the close relationship between the eyes and the vestibular apparatus and in their importance in the control of posture. It follows that visual organs are found almost solely in actively moving animals, while in such as assume a sedentary phase they tend to degenerate and disappear.¹

The stage at which these motorial responses to light evolved beyond purely reflex acts below the level of consciousness and became endowed with awareness is impossible to conjecture. This question has given rise to a controversy which is still unsettled.

In the simple philosophy of Aristotle² and for 2,000 years thereafter no argument arose ; plants had a vegetative soul responsible for growth and repro-

¹ p. 721.

² p. 28.

duction, to animals was added a sensitive soul governing movement and sensation, and to man a rational soul. But doubts occupied men's minds particularly in the seventeenth and eighteenth centuries in the long disputation between the materialistic French Cartesians who followed Descartes (1596-1650) and the English Newtonians who were inspired by Newton (1642-1727) on the one hand, and the mystic German Nature-philosophers on the other, the disciples of Paracelsus in the classical tradition, who found philosophical expression in Leibnitz (1646-1716) and Goethe (1749-1832). To the first the universe was essentially mechanical; to the second not only living creatures but minerals and chemical compounds were permeated by a directive vital force. A middle view was represented by Lamarck (1744-1829) who claimed that the lowest organisms were insensitive and that their conduct was completely governed by external factors, driving forces derived from the environment; but as the evolutionary scale was ascended and a centralized nervous system was acquired, organisms generated their own "sentient intérieur" to a progressively greater degree, thus attaining an ever-increasing measure of self-determination until Vertebrates were reached, at which stage intelligence became possible and ultimately found its fullest expression in Man. Each of these views has been maintained in recent times—the simple reflexology represented by Loeb (1918) and the Russian school (Sechenov, 1863; Bekhterev, 1913; Pavlov, 1926-27) on the one hand, and the purposive or "directive" psychology represented by Whitehead (1929), McDougall (1933) and Russell (1934-45) on the other, wherein vital force has been replaced by the "general drive" of modern biologists, a state of tension or action-energy which activates living organisms. Each view would find its advocates today.

The mechanistic view would place the emergence of visual reflexes into the plane of consciousness as a late development. This attitude found its apostle in Jacques Loeb (1906-18)¹ who considered that all the orientating and instinctive reactions of the lower animals to light or other stimuli were mechanically determined; although in many cases it seems to respond voluntarily and often purposively, the movements of the phototactic animal are those of a robot; it is forced to go where it is taken by its reflexly-driven cilia, legs or wings, an activity in which consciousness or vision has no place. Even an ant with all its proverbial intelligence orientates its journey to light unthinkingly as does a sleep-walker or an automaton² and in this respect is as unteachable as a machine, completely totalitarian and incapable of individual adjustment.

It must be remembered that the new science of cybernetics has demonstrated that similar reactions, sometimes of astonishing complexity, can be carried out by non-vital mechanisms, those curious electro-mechanical first cousins of computing machines, which by a combination of photo-cells, amplifiers, motors and automatic governing devices, can simulate many of the reactions of living things, not in appearance but in behaviour, as they navigate themselves around the play-room of the electronic engineer (see Ashby, 1952; Walter, 1953; and others). Such mock-biological robots, goal-seeking and self-regulatory, capable of the storage of information and possessed of a rudimentary type of memory

¹ p. 28.² p. 68.

maintained by electrical oscillations, have been constructed so that they can explore their environment with an apparent purpose. A photo-cell can serve as a receptor and amplifiers and motors can be interconnected in such a way that a positive taxis (for example) to a moderate light and a negative taxis to bright light (or to material obstacles, gradients, etc.) can endow it with the faculty to discriminate between effective and ineffective behaviour, to seek actively an environment with moderate and optimal conditions, to acquire conditioned reflexes, and even to perpetuate its activity and "feed" itself with electricity by being optically attracted to a charging circuit when its batteries begin to fail.

On the other hand, there are those who consider that such automata have little resemblance to even the simplest living things; their behaviour has only a superficial appearance of being dominated by taxes and kineses, by memory, habituation or trial-and-error learning. The school of biological philosophy formalized by Whitehead (1929), amplified by McDougall (1933) and pursued by such recent writers as Agar (1943) and Thorpe (1956) argues that every vital event is an act of perception, a mental as opposed to a material process; a living organism is essentially something which perceives; its behaviour is not an automatic response to sensory impressions but includes an element of purpose building up primary perceptions into unitary systems in which the whole is different from and greater than the sum of its constituent parts. Such a view, as we have already hinted, tends to pan-psychism, or even to pan-theism: according to it a purely objective biology is sterile; like the warp and woof, mechanism must be interwoven with teleology.¹ While mechanisms may eventually become explicable in physico-mathematical terms, there is no suggestion yet that the subjective concepts of conscious purpose ever will be (Sommerhoff, 1950). But, even although this is agreed, it is to be remembered that there are no grounds for supposing that any well-defined mental content is associated with the reactions of the lower animals comparable to the perceptual experiences of the higher animals.

On the whole it would seem that the matter is not so simple as the more materialistic outlook might suggest. It is true that many of these primitive tropic activities of the animal world can be interpreted as reflexes without motivation, incentive or appreciation; but because there are no discernible conscious accompaniments to many purely reflex acts in man whose apperceptive powers have been translated from the level of ganglia to the cerebral cortex, it by no means follows that there are none in those lowlier organisms the nervous system of which consists only of ganglia and nerve-fibres—or even of an uncentralized nerve-net or nothing at all. It must be remembered that the transference of sensory appreciation to the neopallium occurred late in evolutionary history.² and that although the lower centres in man have

¹ See D'Arcy Thompson (1942).

² p. 542.

become merely relay-stations in this respect, they used to subserve much more important functions. Indeed, in the higher animals—and to some extent also in man—much of mental and most of visual activity, especially those aspects associated with primitive responses and endowed with emotional tone, remain closely associated with the vegetative activities which are integrated in the thalamus. Even in Fishes and Amphibians, vision is entirely unrepresented in the cortex.

Thus although ablation of his occipital lobes deprives man permanently and completely of all sensations of light, the higher mammals are by no means so incapacitated.¹ Most decerebrate Vertebrates will react and exhibit emotions to visual stimuli and even perform complex instinctive reactions without difficulty. So will the headless bee sting with accuracy on irritation (Bethe, 1897) and the clover-fly clean its wings with its legs after decapitation (Sherrington, 1920). A brain, or even a head-ganglion, is thus not a necessary residence for apparently “intelligent” reactions.

Phototactic reactions are “instincts”, that is, adapted reactions of a purposive nature handed down from the previous experience of ancestors; and, as with all instincts, the component afferent impulses have become associated in consciousness and synthesized into a meaningful pattern, a process which necessarily connotes some degree of perception.² As instincts, their usual stereotyped uniformity can be modified by experience provided the modification tends to the well-being of the individual—or the race. The reactions of even the lowly earthworm are amenable to training³; many molluscs are readily trainable; many insects eminently so. Thus the photo-negative cockroach, *Blatella germanica*, can be conditioned to advance towards a light provided it has been taught that a dark and comfortable shelter is placed beneath it (Goustand, 1948). Similarly, as we have seen,⁴ after interference with its receptors or effectors either by partial blinding or by removing some of its legs, the mutilated insect will rapidly modify its reactions and after several trials will learn to orientate itself to light with almost the same accuracy as before. It is thus impossible to say where in the animal scale reactions to light were first associated with conscious awareness; nor can we guess the form such consciousness may take, for like a solid to an inhabitant of Flatland, it exists in a form which cannot be assessed by the measuring instruments at our disposal; we can only reason by inference from an analysis of our own peculiar form of consciousness of which alone we have immediate knowledge. From a study of the sensory capacities of animals few things emerge more certainly than that each species has its own perceptual world (the *Merkwelt* of v. Uexküll, 1921), and that

¹ p. 545.

² See Lloyd Morgan (1896–1912), Jennings (1906), Sherrington (1920), Parsons (1927), and many others.

³ p. 573.

⁴ p. 59.

each of this multitude of worlds bears little resemblance to the environment of the animal as we see it or interpret it in terms of our own *Merkwelt*.

It seems reasonable to assume that the development of vision as a facet of consciousness evolved in three stages. We may surmise that the first conscious appreciation was a mere sentience, crudely vague and undifferentiated, characterized perhaps by a minimum of cognition endowed with a rudimentary affective tone ; it was limited perhaps to an awareness of the existence of light as a change in the environment, tinged perhaps with sufficient affective tone to allow it to be appreciated as pleasant or unpleasant, and endowed with meaning in so far as the organism responded appropriately by motor activity in which initially there was offered the choice only of two alternatives, towards or away from the source of stimulation. We may even surmise as indeed experimental evidence on the amoeba would suggest,¹ that the most primitive sensation was a co-aesthesia without constituent modalities in which the several senses as we know them were merged into a vague and indiscriminate unity, and the stimuli (photoc, chemical, tactile, etc.) which to us are distinct and unrelated were co-equal and additive. Some such concept as the emergence of a consciousness of a lowly type at an early but unknown stage, on the reflex plane or even below, would seem a possible hypothesis, a consciousness at first indefinable and vague but at the same time sufficiently plastic to contain the germ of the elaborate emotional behaviour of the higher animals—so long as we remember that the latter with all its undoubted richness and complexity bears little resemblance to the consciousness of man.

For such a surmise, however, there is no direct evidence; at this level the motor response to stimulation is all we can directly assess. From morphological and behavioural observations, however, we can be more certain that a primitive perception of light emerged with the development of a centralized nervous system in worms²; at this stage in evolution it would seem reasonable to suppose that a mechanism became available for the creation of perceptual symbolism; and at this stage vision undoubtedly became a perceptual process forming part of the conscious life of the animal and capable, at first in a minor degree, of determining its conduct. As we ascend the animal scale the primitive light-sense evolved into a sense of appreciation of the directional incidence of light, of movement, of form, and eventually of colour, until in the Primates the capacity to analyse complex visual patterns became the chief determinant of conduct. In its final development, the first elements of which have been detected in the chimpanzee,³ the sense of vision passed beyond the stage of passively

¹ p. 36. Compare also the integration of phototaxis and galvanotropism seen in certain worms (p. 33).

² p. 572.

³ p. 602.

recording objective appearances in the outside world and emerged as an imaginative and creative sense. This æsthetic quality was certainly a late acquisition acquiring maturity only in man.¹

The extent to which in the animal scale an appreciation of these three progressive stages became a factor in the customary activities of the life of living organisms is a question which must await the acquisition of a much more profound knowledge of their natural history than we at present possess. And—whatever the future may bring forth—the manner of its becoming so is inexplicable by any physico-mathematical techniques we have at our disposal today or will have tomorrow.

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¹ p. 753.

PART II

THE EVOLUTION OF THE VISUAL APPARATUS

THE MORPHOLOGY OF INVERTEBRATE EYES

THE SYSTEMATIC ANATOMY OF INVERTEBRATE EYES

THE EYES OF PROTOCHORDATES

THE EVOLUTION OF THE VERTEBRATE EYE

THE EYES OF CYCLOSTOMES

THE EYES OF FISHES

THE EYES OF AMPHIBIANS

THE EYES OF REPTILES

THE EYES OF BIRDS

THE EYES OF MAMMALS

THE CENTRAL ORGANIZATION OF VISION



FIG. 75.—RICHARD HESSE (1868-1944).

CHAPTER VI

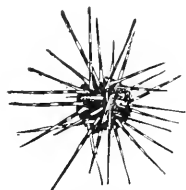
THE MORPHOLOGY OF INVERTEBRATE EYES

RICHARD HESSE (1868–1944) (Fig. 75), one of the greatest of German zoologists, probably contributed more towards the study of the sense organs, particularly the visual organs, of the lower animals than any other single individual. The greater part of his life was devoted to this subject. Professor of Zoology at Tübingen in 1901, he became Professor at the Agricultural School in Berlin in 1909, occupied the Chair of Zoology at Bonn in 1914, and was Professor of Zoology and Director of the Zoological Institute at the University of Berlin from 1926 to 1935. His systematic study of the light-sensitive organs of Invertebrates was largely conducted between 1896 and 1908 and included an immense range of types varying from the relatively simple eyes of worms to the highly developed visual organs of Molluses and Arthropods, an interest which he maintained throughout his long and fruitful life. As will be seen in the following pages, his studies form the basis of our understanding of the astonishing variation in the morphology of the eyes of the Invertebrates. It is surprising how little systematic work has been done on this fascinating subject since his day.

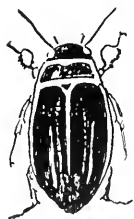
THE GENESIS OF THE EYE

It is evident from the subject-matter of the previous chapters that the eye has evolved from remote and lowly origins, far removed in form and in function from the highly specialized mechanism we find in Man. In the most primitive unicellular organism, as we have already seen in the case of the *amœba*,¹ there is a *diffuse reaction to light* whereby the entire cell, and particularly its superficial layers, in the absence of any apparent specialization of structure responds by a simple alteration of the sol-gel reversibility of the relatively fluid protoplasm. In its earliest form this would seem to be an undifferentiated response common to all stimuli (photie, tactile, thermal, chemical) (Pantin, 1924–26; Folger, 1926–27; Mast, 1926–32). A reaction of this simple nature to light is typical of the Rhizopods, such as the *amœba*, but among multicellular organisms we would expect it to be localized preferentially in the cells on the surface which are exposed to the stimuli of the external world; it thus evolves into a general *dermal photosensitivity*. This may occur sometimes in the absence of known photoreceptors, sometimes in association with them, and it is interesting that even when these are present, the more primitive and less specialized mechanism may dominate the behaviour of the animal in its reactions to light more effectively than the conspicuous receptor organs.

¹ p. 35.



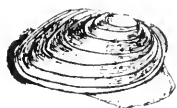
*Diadema
antillarum*



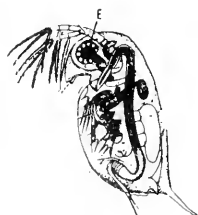
Dytiscus



Myxine



Anodonta



Daphnia

The mechanism of this dermal sensitivity is conjectural. The reaction may be initiated by photosensitive pigments and, although in most cases such have not been identified, they could be present in very small amounts (von Uexküll, 1897). On the other hand, it is conceivable that nerve elements lying subdermally may be directly stimulated, a view for which Millott (1954-57) produced firm evidence in the case of the sea-urchin, *Diadema*. Such a reaction would correspond to the activity of the organelle of the apolar light-sensitive cells of worms, the sixth abdominal ganglion of crayfish and lobsters,¹ and the nerve elements in the diencephalon of lampreys, minnows and ducks.² Again, Bohn (1940) and Viaud (1948) looked upon the reaction as a common property of protoplasm depending on "electrochemical polarization", a property readily evident in lower forms but often neutralized or masked by more potent reactions in higher forms.

Such a dermal light-sensitivity (the DERMATOPSIA of Graber, 1884) is of wide distribution occurring in members of almost all phyla.³ While it is usually diffuse it may be particularly well developed in certain situations wherein its biological utility is greatest, often the fore-part of the animal or in such situations as the region of the spiracles of the abdomen of the larvæ of the water-beetles, *Acilius* and *Dytiscus* (Schöne, 1951). Such a sensitivity is particularly marked and widespread among Echinoderms (Cuénot, 1891); it occurs in some Molluscs, Turbellarians and Annelids, as well as in some Insects, in Cyclostomes (*Myxine glutinosa*, Newth and Ross, 1955), in eyeless cave-fish (Thines and Kähling, 1957) and in blinded cat-fish. The response to dermal sensitivity is, of course, a photokinesis which may be either positive or negative. Thus the eyeless mussel, *Anodonta*, reacts to a passing shadow (Knoop, 1954; Braun and Faust, 1954), blind cavernicolous beetles (*Anophthalmus*) respond to the light of a candle (Marchal, 1910), and after complete blinding some insects, such as cockroaches, will settle preferentially in the dark,⁴ a reaction which may persist even after decapitation,⁵ while others are attracted to light.⁶

It is to be noted that the dermal response to light need not be of the same type as the ocular response; the two may, indeed, be mutually exclusive. Thus it will be remembered⁷ that the flat-worm, *Planaria lugubris*, is positively photokinetic so far as the dermal response is concerned while it orientates itself by a negative phototaxis through the eyes (Viaud and Médioni, 1949). Again, the receptors in the skin and the eyes may show different sensitivities. Thus Viaud (1948) found that in some organisms the maximum response of the dermal mechanism was elicited by wave-lengths at the short end of the visible spectrum (the water-flea, *Daphnia*; the rotifer, *Branchionus*) while the eyes responded preferentially to wave-lengths about the middle of the spectrum. A combination of the two mechanisms in the same organism may thus involve two maxima in the response (as in the fruit-fly, *Drosophila*).

¹ p. 115.

² p. 537.

³ For reviews, see Willem (1891), Dubois (1892), Nagel (1896). See especially Viaud (1948) whose views have already been discussed on p. 31.

⁴ *Blattella*—Graber (1883); *Periplaneta*—Brecher (1929).

⁵ The larvæ of the meal-worm, *Tenebrio*—Tuculesco (1933).

⁶ C. cepillars—Lammert (1925), Süffert (1932), Oehmig (1939).

⁷ p. 4.

Specialization, however, occurred at a very early stage, for some degree of a localization of the sensitivity to light is seen even among Protozoa. The most elementary expression of this advance is the accentuation of photosensitivity in one part of the cell, and since the early response to the stimulation of light was motorial, this occurred particularly in the anterior part of the organism or in close association with the organs of locomotion, as is seen in the eye-spots of Flagellates and Ciliates; an appreciation of directional activity was thereby gained. When unicellular organisms developed into multicellular, however, the subdivision into cells gave the opportunity for more intense specialization, and out of the generalized dermal sensitivity, specific integumentary *light-sensitive cells* were evolved; these again tended to accumulate in localities where the reception of stimuli was of most biological value—towards the head-end of the animal, as in annelid worms, or in association with the motile organs such as the tentacles of Cœlenterates, or the siphon or mantle of Molluscs.

Such a single cell, however, although able to appreciate the presence of light, is unable to form images; for this purpose a number of photosensitive cells must be aggregated together to form an "organ". The most primitive organ of this type is composed of a simple colony of independent cells without functional relationship—the *simple eye* or *ocellus*—and eventually such a grouping of cells became structurally and functionally related in the *compound eye*; in either case the receptor cells were usually provided with a focusing arrangement to concentrate the light and a pigment mantle to absorb any excess. In this way eyes are found in some polychæte worms and higher Invertebrates which from the anatomical point of view can form the basis of vision of varying degrees of sensitivity and resolution.

Throughout Invertebrates there is therefore a wide range of photoreceptor mechanisms; they have, however, one thing in common—that in contradistinction to the "cerebral eye" of Vertebrates, which is essentially of one general type and is developed from the neural ectoderm, with few exceptions (e.g., Rotifera) *they are all derived from the surface epithelium*. It is to be remembered, however, that in some Invertebrates, in addition to the integument and its derivatives, portions of the central nervous system appear to be light-sensitive. This applies, for example, to the sixth abdominal ganglion of the crayfish (Prosser, 1934); in the eyeless white cave crayfish, *Cambarus ayersii*, Wells (1952) found that stimulation of the cerebral ganglion by light results in an increased kinesis without the suggestion of a visual sense. This is analogous to the light-sensitivity of portions of the central nervous system, particularly of the ependymal cells, of some Vertebrates,¹ and the gonadotrophic action of light on the hypothalamus of some birds such as the duck² (Benoit *et al.*, 1952).

¹ p. 537.

² p. 559.



Drosophila



Rotifer

It is interesting that to a certain extent "photoreceptors" may be seen in the vegetable world with an appropriate structural differentiation. Some plant cells, for example, may be raised up and rendered more convex with a lens-like thickening of the cuticle so that they may collect and concentrate the light more easily on the chloroplasts underneath (Haberlandt, 1901) (Fig. 76). This forms a receptor organ comparable to that seen in many animals—a veritable eye.

The range of photoreceptive mechanisms seen in Invertebrates is wide, and far exceeds in its complexity the degree of vision which has hitherto been functionally demonstrated in many species, but at the same time it is probably legitimate to correlate function with structure to some extent. In the Protozoa we presumably have merely a common

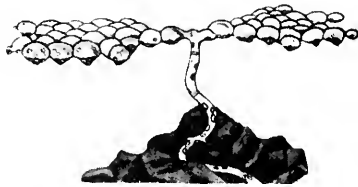
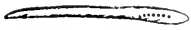


FIG. 76.—PROTONEMA OF *SCHISTOSTEGIA*
OSMUNDACEA.

The feeble light available in the habitat of the plant is concentrated by the lens-shaped cells upon the chloroplasts underneath.

irritability, from which we may deduce a sentience without specific characteristics.¹ With the appearance of multicellular animals specialization became possible so that some of the cells in the outer layer could acquire a specific response to various types of stimuli. When the receptors thus became structurally differentiated, it may be assumed that a corresponding differentiation in function became possible. Four main groups or modalities appeared — mechano-, chemo-, thermo- and radio-receptors; of these the first was probably the most fundamental, but the last, although originally the least important, in subsequent evolution has far transcended the others by virtue of its greater potentialities in being able to project itself, as it were, into the distance. The development of "distance" receptors and of the projicient senses is late.

Indeed, it has been suggested that radio-receptors only acquired their attributes as distance-receptors secondarily and that appreciation of light and darkness originated in a photoreceptor sensitive to a photochemical change in a substance with which it was in contact. The sea anemone appears to possess photoreceptors of this simple kind (von Uexküll, 1909), and a similar faculty is present in the skin of the ammocete larva of the lamprey (Parker, 1903-5) and in numerous Amphibians (Nagel, 1896).



Ammocete larva
of lamprey

This tendency, of course, is not confined to vision. The touch-spots of the skin have been projected in certain Carnivora to the tips of vibrissae so that exploration of the immediate environment is rendered more easy,² while the gloriole mechano-receptors of the organs of Corti respond to vibrations from a wide area in space of an amplitude considerably less than the diameter of the hydrophone atom (von Békésy and Rosenblith, 1951). Similarly, the heat-spots

¹ p. 36.

² For a general study, see Fitzgerald (1940).

of the skin become projected in the temperature receptors seen in vipers in which a facial pit-like "eye" has developed for the reception of infra-red radiation (Bullock *et al.*, 1952-56).¹ The eye, of course, has transcended all other organs in this respect, projecting itself to astronomical distances and responding to a few quanta of luminous energy.

Originally it is probable that within the main groups, or modalities, appreciation was relatively undifferentiated²; for example, a usual accompaniment of the radio-receptors is an absorbing pigment, and it is possible that the early pigmented cell responded to thermal energy as well as to luminous radiation. Subsequent evolution, both in the receptors and in their cerebral connections, determined not only an increase in the number of modalities (touch, temperature, smell, sight, hearing) but eventually led to the differentiation of various individual receptors within the same modality, thus allowing the emergence of qualities within a modality, such as colour within the modality of sight.

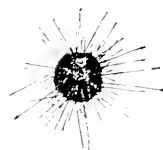
PIGMENTS

PIGMENT is a common feature of photoreceptors of all types; indeed, Bernard (1897) suggested that light-sensitive cells first arose as modifications of the epidermis induced by crowding of pigment granules in situations which were most frequently and brilliantly illuminated. The physical energy of light can be converted into physiological activity only in so far as it is absorbed, and the primary function of the deposition of pigment in the neighbourhood of light-sensitive areas is to serve as an absorbing agent; a further development is the initiation of a specific photochemical reaction.

In its simplest form, pigment may aid the general dermal sensitivity to light, a function well illustrated in Echinoderms. Thus the entire surface of the sea-cucumber, *Holothuria*, is photosensitive and is coloured by two greenish-yellow pigments; the reaction of the animal varies with the amount of pigment present, for young and lightly pigmented individuals are poorly light-sensitive while heavily pigmented adults are markedly so (Crozier, 1914-15). Again, the sea-urchin, *Centrostephanus longispinus*, shows a high light-sensitivity in the violet spicules around the anal orifice whence a purple pigment can be extracted (von Uexküll, 1900)—an early example, incidentally, of the frequent aggregation of sensory organs around the body orifices. When, however, specific light-sensitive organs are developed, pigment is concentrated in their vicinity—melanin as an absorbent and visual pigments as sensitizers. All these pigments are synthesized by special cells called CHROMATOBlasts (χρῶμα, colour; βλαστός, a sprout).



Holothuria



Centrostephanus

¹ See further, p. 600

² p. 109.

MELANIN

MELANIN ($\mu\epsilon\lambda\alpha\varsigma$, black) is the common dark brown pigment ; it is elaborated locally by the organism from a colourless precursor found in the nucleus of special cells (MELANOBLASTS). Very inert chemically, it acts merely as an absorbing agent.

Melanin is a close relative of adrenalin and was originally thought to be derived from the blood (Scherl, 1893 ; Ehrmann, 1896 ; Augstein, 1912), but at an early date it was shown to have nothing in common with the derivatives of hæmoglobin. A cellular origin therefore being necessitated, Kromayer (1893) and Hertwig (1904) suggested that it was derived from the nucleus, and Meirowsky (1906) narrowed this down to the nucleolus owing to the demonstration of large quantities of pyronin (a nuclear constituent) in melanotic cells, a view which appeared to be substantiated by the finding of this material in melanotic tumours by Rössle (1904). A further advance was made by von Szily (1911) who showed that the pigment was formed from a colourless precursor by the action of a ferment. Masson (1913) established that the action was oxidative in nature, and Bloch (1917) cleared up the matter by demonstrating that the cells of pigmented regions contain a specific intracellular oxidase. Bloch then isolated from the embryo of the broad bean 3-4-dihydroxyphenylalanine, a substance which he conveniently called "dopa", and showed that it was readily changed by this oxidase to melanin. When this substance is added to the epidermal cells of skin in frozen formalin-fixed sections, granules of melanin are formed (the "dopa reaction"). A large number of the groupings in the protein molecule form coloured products on oxidation (tyrosine, phenylalanine, tryptophane, etc.), and it seems obvious that melanin, like adrenalin, is formed as an end-product from one of these chromatogen groups. Bloch concluded that the colourless "mother substance" (or melanogen) is almost certainly either identical with or related to "dopa"; this colourless substance is brought by the blood-stream to the cell ; here it meets the "dopa-oxidase" and thus is turned into the coloured pigment melanin.

THE VISUAL PIGMENTS

Photochemical and sensitizing reactions in both plants and animals, both phototactic and visual, depend almost universally upon one distinctive and compact group of substances, the CAROTENOIDS—a striking indication of the close evolutionary relationship between phototropism and vision. These form a number of pigments varying in colour from red to yellow, fat-soluble and highly unsaturated, occurring alone or as the prosthetic groups of proteins ; all of them seem to be related to the chromophore moiety of visual purple and are identifiable by their absorption spectra, the maxima of which usually lie somewhere towards the blue side of the mid-region of the visible band. As we have seen in a previous chapter¹ they also have a wide integumentary distribution among many species where they may play a decorative part in the coloration of the animal. Their high concentration in the sex-glands (the interstitial cells of the gonads, the

¹ p. 87.

adrenal and renal cortex) is a further point of association between the action of light and sexual activities¹ (Goodwin, 1950).

In the vegetable kingdom the predominant carotenoids are β -CAROTENE, $C_{40}H_{56}$, and XANTHOPHYLL, $C_{40}H_{54}(OH)_2$ —yellow pigments absorbing preferentially blue light with absorption spectra quite different from that of chlorophyll. The latter and its relatives are active in the photosynthesis of plant metabolism and have no effect upon phototropic responses; the former and its derivatives are concerned in photoreception in systems mediating orientation to light, they are peculiarly susceptible to the blue end of the spectrum, and are found only in the photosensitive parts of plants, such as the oat coleoptile

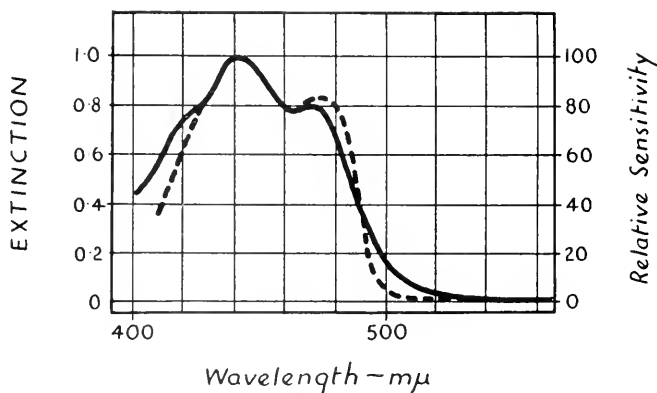


FIG. 77.—SPECTRAL SENSITIVITY OF THE PHOTOTROPIC BENDING OF PLANTS, AND THE ABSORPTION SPECTRA OF THE ASSOCIATED CAROTENOIDS.

Absorption spectrum (extinction) of the total carotenoids of the etiolated oat coleoptile, *Avena*; continuous line (after Wald). Relative spectral sensitivity of the oat shoot; broken line (after Johnston).

(Voerke, 1933; Castle, 1935; Bünning, 1937; Wald, 1943). Wald (1945–46) brought out this relationship dramatically by a study of the absorption characteristics of the phototropic response; he found that the active spectrum of the phototropic bending of the seedling of the oat, *Avena*, was maximal in a blue light of 440 $m\mu$ and corresponded very closely with the absorption spectrum of the carotenoids extracted from the coleoptile (Fig. 77).

The phototactic movements of animals, so far as they have been investigated, are also determined by carotenoids but in these the single maxima of absorption are displaced to wave-lengths considerably longer than those associated with the phototropic bending of plants (473 to 534 $m\mu$) (Mast, 1917; Laurens and Hooker, 1920; Luntz, 1931). The pigment responsible for phototactic activity in a number of the green

¹ p. 16.

Flagellates (*Euglena*, etc.) has been identified as ASTAXANTHIN (dihydroxy di-keto β -carotene, $C_{40}H_{52}O_4$) (Tiseher, 1936-38; Kuhn *et al.*, 1939); this pigment is found only in animal tissues, is produced by the modification of ingested plant carotenoids, and, depending on its chemical nature, may range in colour from blue to red with varying characteristics of absorption. The pigments associated with the photoreceptors of the lower Invertebrates have not been fully investigated, but the available evidence indicates that the phototropic responses of the polyps of Cœlenterates¹ and the siphons of clams,² as well as the phototactic activity of worms,³ are also mediated by pigments of the astaxanthin type (Fig. 78).

On the other hand, when image-forming eyes are reached in

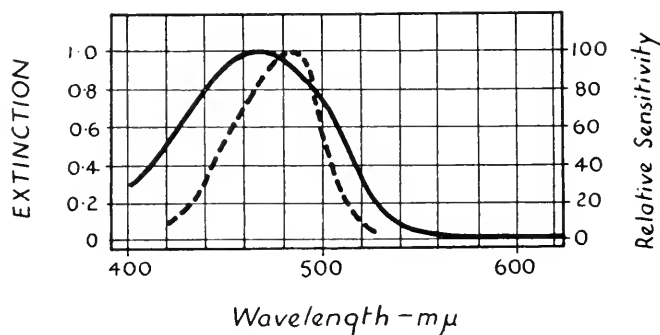


FIG. 78.—SPECTRAL SENSITIVITY FOR PHOTO-ORIENTATION OF THE GREEN FLAGELLATE.

Absorption spectrum (extinction) for astaxanthin dissolved in hexane; continuous line (after Wald). Relative spectral sensitivity of *Euglena viridis*; broken line (after Mast).

Molluscs and Arthropods, the power has been gained to degrade vegetable carotenoids into the VITAMIN A SYSTEM. Thus among Molluscs, the retina of the squid, *Loligo pealii*, has been found to have considerable quantities of retinene₁ and vitamin A₁ which, combined with a specific protein, produces a pigment with absorptive characteristics resembling those of rhodopsin (Wald, 1941; Bliss, 1943-48; St. George and Wald, 1949; Hubbard and St. George, 1956). It would appear that in the squid this reddish photopigment is a non-photosensitive type of rhodopsin, for which reason it was distinguished as *cephalopsin* by its discoverer (Bliss, 1948).

¹ Hydras of *Sertularia* and *Eudendrium*, maximum absorption 474 mμ, Loeb and Wasth (1915).

² *Mytilus*, maximum absorption 490 mμ, *Pholas*, maximum absorption 555 mμ, Hecht (1917).

³ The earthworm, *Lumbricus terrestris*, and the larvæ of the marine worm, *Arenicola*, maximum absorption 483 mμ, Mast (1917).

Vitamin A₁ has also been isolated in quantity from the eyes of a number of marine Crustaceans,¹ and the occurrence of this photochemical system in the eyes of the king-crab, *Limulus*, and of Insects has been corroborated by studies of their spectral sensitivity (Graham and Hartline, 1935; Jahn, 1946; Granit, 1947; Jahn and Wulff, 1948; and others) and also by behavioural experiments (Weiss, 1943). It is evident that more than one type of pigment exists belonging to the vitamin A₁ family; thus among the shrimp-like euphausiid Crustaceans, Kampa (1955) isolated a pigment (*Euphausiopsin*)² with a maximum absorption of 462 mμ, and in the deep-sea prawn, *Pandalus*, an isomer was detected by Lambertsen and Braekkan (1955). It is true that in some of these organisms astaxanthin may also be found³

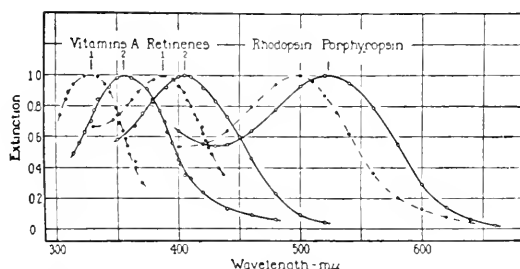


FIG. 79.—SPECTRA OF THE RHODOPSIN AND PORPHYRPSIN SYSTEMS

Direct spectra of crude preparations from the retinae of the marine scup (broken lines) and the freshwater calico bass (continuous lines). Rhodopsin and porphyropsin are dissolved in 1 per cent. aqueous digitonin solution, the retinenes and vitamins A in chloroform. All maxima have been brought to the same height to facilitate comparison (Wald).

but this pigment appears to take no part in the visual process and is also distributed throughout the integument (Wald, 1941-46).

Among Vertebrates the primitive Cyclostomes still retain the vitamin A₁ system (visual purple) (Steven, 1955) associated with their retinal rods, as also does the majority of marine fishes⁴ so far examined; on the other hand, most fresh-water fishes⁵ possess a different system based on vitamin A₂ and retinene₂. In Amphibians and higher

¹ Crabs, lobsters and others, Wald (1945-46), Fisher *et al.* (1952-55).

² Possibly related to or identical with the pigment absorbing maximally at 467 mμ described by Dartnall (1952) in the tench.

³ As in the fresh-water crayfish, *Cambarus virilis*; the shrimp, *Aristeomorpha*, Grangaud and Massonet (1950).

⁴ Exceptions are found, for example, among the wrasse fishes (*Labrus bergyllta* and *Tautoga onitis*), the eyes of which have a pigment based on the vitamin A₂ system (Bayliss *et al.*, 1936; Dartnall, 1955).

⁵ An exception is the fresh-water bleak, *Alburnus lucidus*, which has, in addition to two pigments based on vitamin A₂, another probably based on A₁ (Dartnall, 1955). It is to be remembered, however, that only a few species have hitherto been examined so that further investigation may weaken this generalization.

forms in the vertebrate phylum the vitamin A_1 system is again encountered. Wald (1939-56) considered that two specific pigments were concerned—rhodopsin (visual purple) with the vitamin A_1 system and porphyropsin (visual violet) with the vitamin A_2 system (Fig. 79). Evidence is rapidly accumulating, however, that the matter is not so simple, for it would appear that each of these does not represent a single specific pigment; both vitamins A_1 and A_2 can exist as a number of isomers some of which combine with suitable proteins to yield photosensitive pigments of distinctive absorptive properties, several of which have already been discovered. Rhodopsin should therefore be interpreted as a generic name for all visual pigments associated with the rods based on vitamin A_1 , while porphyropsin is best similarly interpreted as embracing several rod-pigments based on vitamin A_2 (see Dartnall, 1957).

The photosensitive pigments so far claimed—although with little substantial evidence—to be present in vertebrate cones—iodopsin associated with the vitamin A_1 system and cyanopsin associated with vitamin A_2 —are also related carotenoid-proteins (Wald, 1937-55; Bliss, 1946)¹; on the other hand, accessory needs in the visual system such as the yellow pigment of the human macula are said to be met by xanthophyll—the intact carotenoid which mediates photo-reception in plants.

The multiplicity of pigments of these two general types associated with the visual system is becoming increasingly apparent, and odd varieties have been discovered in special circumstances, differing considerably from the main groups. As we have seen, fresh-water fish usually have a pigment of the porphyropsin family, salt-water fish of the rhodopsin family; euryhaline and migratory fishes which adapt themselves to both fresh and salt water therefore present an interesting problem. Since their spectral absorption curve is intermediate between that of rhodopsin and porphyropsin, Wald (1941) concluded that their retinae contained a mixture of both; but it has been shown by Munz (1956) that in one at least of these fishes (the mud-sucker, *Gillichthys mirabilis*) the retina contains a single homogeneous pigment characteristic of the retinene₁ type with an absorption maximum intermediate between the two main groups (512m μ). Again, the gecko (*Gekko gekko*) has an unusual spectral sensitivity curve, similar to the human scotopic curve but with its maximum displaced 20 to 30m μ towards the red end of the spectrum (Denton, 1956). Retinal extracts from the Australian gecko, *Phyllurus miltii*, have shown the presence of an unusual pigment with an absorption maximum at 524m μ , typical of the retinene₁ system but intermediate between the rhodopsin of the rods and the iodopsin of the cones (Crescitelli, 1956). This is interesting in view of the theory that the rods of this nocturnal animal may be transmutations from the cones of ancestral diurnal lizards.²

Pigments of unknown composition and unknown function which appear,

¹ In the eyes of primates three pigments have been detected: chlorolabe (a green-absorbing pigment), erythrolabe (red-absorbing), and cyanolabe (blue-absorbing). See Vol. IV, p. 252.

² p. 252.

however, to differ from the preceding, have been found in the eyes and also in the integument of Arthropods among which they appear to have a wide distribution. They have been most fully studied in the eyes and integument of Insects and were first cursorily examined by Chauvin (1938-41). Becker (1939-41), studying these pigments in the ommatidia of a number of insect species, gave them the generic term OMMOCHROMES and subdivided them into OMMINS and OMMATINS. In certain insects, such as the fruit-fly, *Drosophila*, for example, he described a purplish-red pigment (erythrommatin) and a yellowish-brown (phaeommatin). During pupal development the brown pigment appears first and the red later, their appearance being determined by hormones, and one or other or both of the pigments may be absent in certain stocks, the eyes appearing respectively brown, red or white.¹ At a later date, however, Goodwin and Srisukh (1950) and Goodwin (1950), working on locusts (the desert locust, *Schistocerca gregaria*, and the African migratory locust, *Locusta migratoria*), concluded that these pigments represented a redox complex, yellow when oxidized and wine-red when reduced. For this variable pigment, or group of very closely related pigments which are at the moment indistinguishable, they suggested the name INSECTORUBIN, in view of its widespread distribution among insects. Whatever its chemical nature, it is very resistant to chemical attack, but has been isolated as a reddish-brown powder which quickly changes into a stable dark brown powder reminiscent of melanin, and shows characteristic absorption spectra differing according to the method of extraction, whether measured in the fresh extract or in the reduced or oxidized form.

Related pigments with similar absorption curves have been described in crustaceans (the shrimps, *Leander* and *Crangon*—Polonovski *et al.*, 1948 ; the fresh-water Amphipod, *Gammarus pulex*—Michel and Anders, 1954).

Such is the general evolutionary story of the photopigments ; it is a large subject which will be discussed more fully when we deal with the physiology of vision in a subsequent volume. In passing, however, it is interesting to note that many years ago Patten (1886) put forward the theory that photoreceptors were originally evolved, not as sentient organs, but as receptors of light-energy for metabolic purposes as occurs in plants. He called them HELIOPHAGS. The theory, however, in its time raised a storm of criticism and never received credence ; the most cogent evidence against it is the completely different chemical nature of chlorophyll and the carotenoids and the contrast in their functions—metabolism on the one hand, and photoreception or integumentary coloration on the other.

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THE STRUCTURE OF INVERTEBRATE EYES

We are now in a position to study the various types of photo-receptors found among Invertebrates. In unicellular organisms the diffuse sensitivity to light evolves into the localized sensitivity of an "eye-spot"; in multicellular organisms the diffuse dermal sensitivity evolves into the specialization of certain epithelial cells as specific photoreceptors.

EYE-SPOTS : STIGMATA

The earliest stage in the evolution of an eye is seen in unicellular organisms in which a small area of the protoplasm is differentiated to become specially sensitive to light: this development is seen in actively motile ciliate and flagellate Protozoa, and since in these organisms light serves not as a visual but as an orientating stimulus, the specialized area is always in close association with the cilia or flagella. Among Ciliates such specialization is primitive; thus without observable structural differentiation, the oral surface of *Stentor coerulesus* is more photosensitive than the aboral so that, as the organism rotates while swimming, successive exposures of these two areas determine a negative klinotaxis, orientating it away from the light (Jennings, 1904; Mast, 1906-11).¹ In Flagellates, however, a degree of structural differentiation appears which is sufficient to dignify the organelle thus formed with the name of an EYE-SPOT or STIGMA ($\sigma\tau\acute{\iota}\gamma\mu\alpha$, a spot); there is a light-sensitive area, a mass of pigment which serves to make the organelle a directional detector useful in phototaxis, and occasionally a refractile structure which serves to concentrate the light, thus acting as a lens.²

The stigma of the common green protozoon of ponds, *Euglena*

¹ p. 49.

² As occurs in the Algae, *Cladophora* and *Gonium* (Mast, 1916).



Stentor

viridis, is of the simplest variety (Fig. 80) ; the entire structure is about 5μ in diameter (Franz, 1893). The base of the single flagellum shows a thickening just anterior to its bifid root in the cavity of the reservoir ; it would seem that this is the photoreceptive area and it is

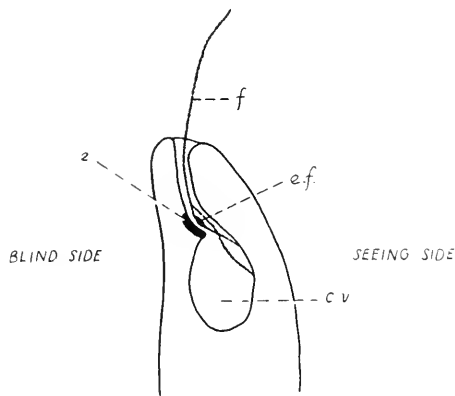


FIG. 80.—THE EYE-SPOT OF *EUGLENA VIRIDIS*.

A side view of the anterior end of the flagellate. *f*. The flagellum with an enlargement, *ef*, which constitutes the photoreceptive area. The two roots of the flagellum are anchored in the large contractile vacuole (*c.v.*). Opposite the sensitive area is a shield of pigment (*e*) (after Wager, 1900).

flanked on one side by a shield of the red carotenoid pigment, astaxanthin (Engelmann, 1882 ; Wager, 1900 ; Mast, 1911–38 ; Buder, 1917 ; Tischer, 1936–38 ; Kuhn *et al.*, 1939). It is interesting that Ehrenberg (1838), who first described this flagellate, assumed that the pigmented area was light-sensitive and considered that it constituted the most primitive eye in nature and called it the *eye-spot* ("Augenfleck"). It seems more probable, however, that it serves as an absorbing agent, shielding the flagellar swelling from incident light on one side and allowing it to be exposed on the other, so that as the organism rotates in swimming, the alternating stimulation and shading of the stigma affect the beat of the flagellum and directional phototaxis is attained.¹

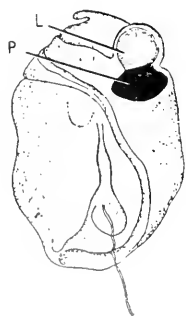


FIG. 81.—THE EYE-SPOT OF *PUCCINELLIA*.

Showing the large pigmented area, *P*, and the lens, *L* (after Schütt).

The instability of such an eye-spot is interesting. The Pringsheims (1952) found that if *Euglena gracilis* were grown at temperatures below the optimum the pigment was lost and an apoplastidic race was produced in which the stigma disappeared if the organism were kept in the dark ; once lost, the eye-spot did not reappear.

In certain Dinoflagellates, organisms which form an important part of the plankton of lakes and the sea, the

¹ p. 48.

stigma may be more complex. In *Pouchetia*, for example, the pigment is arranged in the form of a cup-shaped mass the opening of which is covered by a refractile structure, while within the cup, between the primitive lens thus formed and the pigment, lies the light-sensitive protoplasm (Fig. 81) (Schütt, 1896) ; occasionally in the marine forms this structure is of such a size that it has been called an ocellus, but it is acellular. In all these cases the organelle combines photosensitivity with directional detection in order to perform its phototactic function.

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LIGHT-SENSITIVE CELLS

Once multicellular organisms evolved, the obvious specialization occurred whereby certain cells acquired a special sensitivity to light ; as would be expected, they were ectodermal cells initially developed in the surface epithelium although on occasion they migrated below the surface layer. Such cells may be found alone or may occur in association with others to form an eye ; and in either case they may assume several forms usually with well-defined characteristics, including a specially sensitive receptor as well as an arrangement to conduct away the excitation. Frequently the cell is associated with pigment which serves as an absorbing agent, a function which becomes all the more important when the sentient cells sink below the surface, in which case the receptive pole is frequently surrounded by a pigment mantle (Fig. 82). While thus aiding the receptor mechanism, an absorbing pigment mantle is not essential and, indeed, is frequently absent.

The light-sensitive cell usually assumes a specialized form which may be differentiated into two main types. In the first and more common type two poles are distinguished—a distal to receive the stimulus of light and a proximal to conduct away the excitation. In the fully developed *bipolar cell*, therefore, three regions are apparent : a receptor or end-organ, a cell body with the nucleus, and a proximal prolongation into a conducting fibre.

The receptive end-organ of the cell is often found to assume a complicated form ; sometimes it is provided with digitations, presumably in an attempt to increase the receptor surface (Fig. 87) ; more frequently it undergoes specific modifications which can be classed as belonging to two main types, cilia and rods, the second presumably a

FIGS. 82 TO 85.—TYPES OF BIPOLAR VISUAL CELL.



FIG. 82.



FIG. 83.



FIG. 84.



FIG. 85.

FIG. 82.—The visual cell of the edible snail, *Helix pomatia*, showing cilia (after Hesse).

FIG. 83.—The visual cell of the grey slug, *Limax maximus*, showing elongated end with cilia (after Hesse).

FIG. 84.—The visual cell of the marine worm, *Planaria torva*, showing brush-like border (after Hesse).

FIG. 85.—Rod-like visual cell of the Tabanid fly, *Chrysops marmoratus* (after Ciaccio).

specialized derivative of the first.¹ CILIA (Figs. 82 and 83) are found in many ectodermal cells and form an important differentiation of several types of sensory cells, and it may be, as Hesse (1902) surmised, that they represent the distal terminations of bundles of the "neuro-fibrillae" which form the primitive conducting mechanism²; a similar configuration is seen in cells with a striated or brush-like border (Fig. 84). RODS (OR RHABDITES) appeared originally as simple but stouter cylindrical prolongations of protoplasm, clear and refractile in nature, which in subsequent evolution have undergone innumerable specializations (Fig. 85); they are found in worms, Arthropods, and Molluscs, and they attain their highest differentiation in the rods and cones which form the unique receptor apparatus in the eyes of Vertebrates.

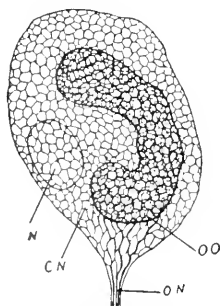


FIG. 86.—APOLAR VISUAL CELL.

A light-sensitive cell in the earthworm, *Lumbricus terrestris*, stained with silver nitrate. N, nucleus; ON, optic nerve which breaks up into a network of neurofibrils, CN, throughout the cytoplasm; O, optic organ covered by a denser network of neurofibrils to form the retinella (after W. N. S. P. 1902).

¹ p. 243.

² See Worley (1933-41).

peculiarly shaped ellipsoidal mass—the OPTIC ORGANELLE (the “Binnenkörper” of Hesse; the “Glaskörper” of Apathy, 1897)—distinctly marked off from the rest of the cytoplasm by its deeper staining, occupying the centre of the cell and crowding the nucleus to one side; it is made up of a clear hyaline-like structure (a “lens”) surrounded by a dense neurofibrillar network (the RETINELLA). Hess (1925) found experimentally that no matter from which direction light was directed onto the cell, the “lens” brought it to a focus on the surrounding network of the retinella, a circumstance which suggests that the hyaline mass focuses the light which induces a direct stimulation of the nerve-fibres, possibly by a photo-electrical rather than a photochemical effect.

Depending on the arrangement of these cells singly or in communities to form an organ, invertebrate eyes may be classified morphologically as follows.

I. The SIMPLE EYE OR OCELLUS.

1. The unicellular eye.

- (a) epithelial,
- (b) subepithelial.

2. The multicellular eye.

- (a) the subepithelial eye,
- (b) the epithelial invaginated eye.
 - (i) the flat eye.
 - (ii) the cupulate eye,
 - (iii) the vesicular eye.

II. Intermediate forms.

- (a) The aggregate eye.
- (b) The composite ocellus.
- (c) The simple ommatidial eye.

III. The COMPOUND EYE.

The Simple Eye

A simple light-sensitive cell, an ectodermal cell differentiated from its neighbours in order to receive incident light and transmit a physiological impulse, ranks as a very primitive type of eye. With single cells, each of which is responsive merely to the presence of light, a light-sense may exist, but no definite image such as is necessary for the development of the visual sense can be formed. If, however, these cells multiply and group together in clumps to form an “organ”, some conception of an object may be realized and a primitive directional analysis may be made of visual space. Each single constituent cell, it

is true, merely records the sensation of light, but the summation of all their individual sensations will give an elementary mosaic or pattern of light and shade with a consequent impression of the external world. So long as the component cells of the group retain their individuality and act independently of each other, they may be considered to form a "simple" eye. The SIMPLE EYE or OCELLUS (dim. of *oculus*, eye) may therefore be defined as a *single light-sensitive cell or group of such cells acting without functional association*.

THE UNICELLULAR EYE

Single cells which are responsive to light ("cellules visuelles" of Apathy, 1897; "Photores" of Beer, 1901) were first adequately described by Richard Hesse (1896) as occurring in the epidermal layer of worms; he called them "Sehzellen", but since in many cases they appreciate the presence of light for the purposes of phototactic reactions and are probably not associated with a visual sense as the term is generally understood, we shall call them LIGHT-SENSITIVE CELLS. Shortly thereafter they were found in a large number of animals, sometimes scattered about indiscriminately but usually aggregated in those regions where they are of most importance to the organism. Thus in clams they are confined to the siphon, in some shell-fish are arranged like a coronet around the edge of the mantle, and in annelid worms they are concentrated at the two extremities, particularly the anterior.¹

Unicellular eyes may assume either of the two forms of light-sensitive cell we have already discussed—the bipolar form with a specialized sensory termination or the apolar form characterized by an intracellular organelle.

SINGLE BIPOLAR LIGHT-SENSITIVE CELLS are usually provided with a ciliate or brush-like border and are associated with pigment, usually placed as a cap around the light-sensitive end of the cell. They are seen in the unicellular photoreceptors of the larvæ of certain sponges (*Leucosolenia*, Minchin, 1896) and in Rotifers, but occur most typically among worms. Examples of this are the light-sensitive cells of *Tristomum papillosum*, a Trematode parasitic on marine fishes (Fig. 87), or in *Polyophtthalmus pictus*, a sedentary Polychæte which abounds in the Bay of Naples (Hesse, 1899–1908).



Leucosolenia



FIG. 87.—UNICELLULAR EYE OF THE TREMATODE WORM, *TRISTOMUM PAPILLOSUM*.

is interesting that the most primitive "cerebral" eye coordinates, seen in the neural tube of *Amphioxus*²

The cell is provided with a crenated border and pigment mantle (after Hesse).

¹ p. 190.

² p. 230.

is similarly a single photosensitive neural cell associated with a pigment mantle (Fig. 238).

SINGLE APOLAR VISUAL CELLS are typified in the light-sensitive organs of the earthworm, *Lumbricus terrestris*; these have received closer study than those of any other species (R. Hesse, 1894-97; Beer, 1901; Kowalski, 1909; W. N. Hess, 1924-25) (Figs. 86 and 88). They are found in two sites—in the epithelium and in association with the nerves immediately underneath; it is probable, as has been shown in the medicinal leech (Whitman, 1893), that the latter originated in and migrated from the epidermal layer. In appearance they are distinctive. The superficial cells are small and rounded, lying at the base of the epithelium and into each the subepithelial nerve-net sends a nerve-fibre which breaks up into a network of neurofibrils surrounding the ellipsoidal optic organelle¹; the subepithelial cells clumped around enlargements of the nerve plexus are similar in type and presumably in function. It is interesting that a dense layer of pigment lies under the epithelium apparently unassociated with the light-sensitive cells; but as they traverse this layer and run into the epithelium, the nerves make pinpoint openings in the dense pigmentary blanket so disposed that incident light will enter, dorso-anteriorly at the anterior end of the worm and dorso-posteriorly at the posterior end, and will thus strike the subepithelial cells directly as either extremity emerges from the burrow.

The light-sensitive cells of leeches are also of a very similar type, each containing an identical optic organelle supplied with a nerve fibre from the dorsal ganglion (R. Hesse, 1897). They may occur as isolated cells just below the epithelium or may lie in association with other sensory cells.² Light-sensitive cells identical with those of the earthworm are also found in lamelli-branch molluscs; thus in the clam, *Mya arenaria*, they are seen, plentifully supplied with nerves, lying just beneath the epithelial layer on the inner surface



Lumbricus

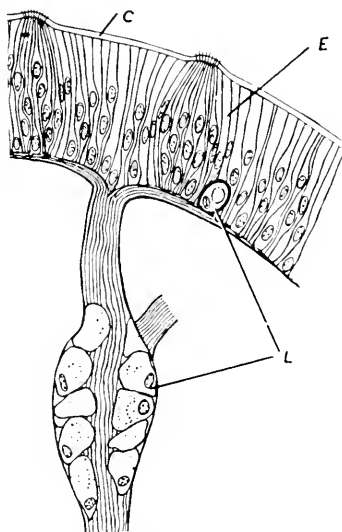


FIG. 88.—SINGLE LIGHT-SENSITIVE CELLS IN THE EARTHWORM, *LUMBRICUS TERRESTRIS*.

The photoreceptor cells, L, lying in the basal region of the epidermis, E, and also in enlargements of the nerve in close relation to the epidermis. The nerve is seen to spread out beneath the epithelium as a subepidermal nerve plexus, the fibres of which go to the photoreceptor cells. C, cuticle (after W. N. Hess).



Mya arenaria

¹ p. 128.

² p. 133.

of the siphon; again, each contains an optic organelle with a surrounding nerve-plexus (Light, 1930). It is interesting that somewhat similar cells, presumably sensitive to light, have been described in the epidermis of the tail of the ammocete larva of the lamprey (Steven, 1951).¹

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 Beer. *Wien. klin. Wschr.*, **14**, 255, 285, 314 (1901).
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J. exp. Zool., **69**, 105 (1934).
J. cell. comp. Physiol., **5**, 53 (1934); **18**, 187 (1941).

THE MULTICELLULAR SIMPLE EYE

While the most primitive example of the simple eye is represented by a single light-sensitive cell, the next obvious development is the association of a group of epithelial cells each reinforcing the effectiveness of the others. For this purpose several evolutionary lines have been followed so that eventually the end-organ appears to reach a degree of complexity greater than the analysing capacity of the nervous organization. Efficiency is enhanced not only by the progressive development of the capacity to form detailed images as the number of sensory cells increases, but also of the ability thereby obtained to localize the stimulus in space and analyse the visual field (a DIRECTIONAL EYE). The association of pigment forming an absorbent screen within or around the sensory cells is a constant feature, while the efficiency of the organ is further increased by the development of a focusing apparatus. To this end a wide variety of optical mechanisms is exploited varying from a pin-hole to a lens-system of progressive elaboration until, in Cephalopods, a dioptric mechanism comparable to that of Vertebrates is reached. The inner ends of the sensory cells are prolonged to form elongated processes or nerve fibres which leave the deep surface of the ocellus to join a subepithelial plexus or a ganglion.

The sensory cells usually remain in association with the surface layer but occasionally migrate inwards to the subepithelial tissues; and since the latter type of ocellus undergoes less evolutionary development than the former, we will discuss it first.

The Subepithelial Eye

The migration of a number of light-sensitive cells from the surface with their aggregation in the subepithelial tissues to form a subepithelial eye always results in an organ of a very elementary type.

¹ p. 263.

These cells may belong to either of the two main types we have just discussed. In the first place, we have already seen in the case of the earthworm that an aggregation of *apolar cells* with a central organelle in the cell-body may migrate from the surface epithelium to form a subepithelial mass in association with the nerve fibres (Fig. 88). Subepithelial eyes formed by the clumping together of a multitude of visual cells of this type within a dense pigmentary mantle are found in certain leeches.

FIGS. 89 AND 90.—THE SENSORY ORGANS OF THE MEDICINAL LEECH, *HIRUDO MEDICINALIS*.

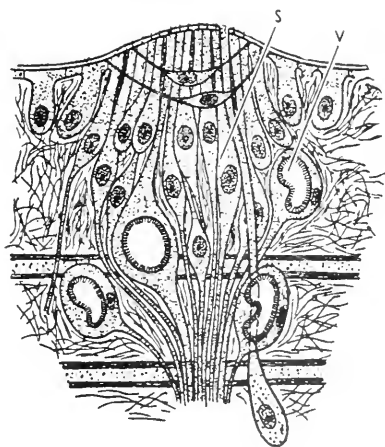


FIG. 89.—The sensory organ of the intermediate segments consists of a collection of undifferentiated sensory cells, S, among which are seen the large light-sensitive cells, V (4 in the figure), with the kidney-shaped hyaline optic organelle (after Bütschli).



FIG. 90.—Each "eye" situated in the anterior segments consists of a cluster of apolar cells provided with optic organelles, the whole being enclosed in a pigment mantle through which the nerve fibres travel, and lying beneath the surface epithelium (schematic after Hesse).

The ocelli of the medicinal leech, *Hirudo medicinalis*, are of unusual interest since they show all stages of evolution from a unicellular to a multicellular eye. As we have noted,¹ typical apolar light-sensitive cells may occur lying singly, deep in the epithelium. On the dorsal surface of the intermediate segments of the animal there are paired clusters of undifferentiated sensory cells derived from the epithelium, each cluster forming a segmental sensory organ the function of which seems to be essentially tactile; among these cells there are several typical light-sensitive cells so that the colony presumably has a dual function (Fig. 89). On the anterior five segments these clusters of cells are purely visual and are clumped together in a cylindrical mass at right angles to the surface enclosed in a dense pigmentary mantle, forming subepithelial eyes (Fig. 90)

¹ p. 131.



Hirudo

*Haemadipsa*

(Whitman, 1889-93 ; Maier, 1892 ; Hesse, 1897-1902 ; Bütschli, 1921). In the land-leech, *Haemadipsa*, the ordinary segmented papillae more closely resemble eyes since the visual cells are associated with pigment (Bhatia, 1956).

In the second place, *bipolar cells* with a ciliate or brush-like receptor and a proximal nerve fibre may similarly migrate into the subepithelial tissues, aggregating into a cluster in association with a mantle of pigment cells. These are seen typically in the leaf-like turbellarian and the ribbon-like nemertine worms (Figs. 91 to 93). In these, the eye consists merely of one or a number of elongated visual cells with a distal ciliated border, the fibrillar terminations of which run proximally to form an optic nerve ; the organ lies under the

FIGS. 91 TO 93.—SUBEPITHELIAL EYES (after Hesse).

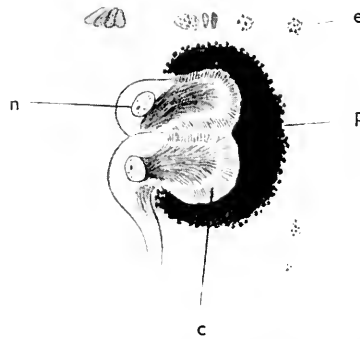


FIG. 91.—The eye of the turbellarian worm, *Planaria torra*, consisting of two light cells with cilia (*c*), nucleus (*n*) and pigment mantle (*p*), the whole lying underneath the epithelium (*e*).

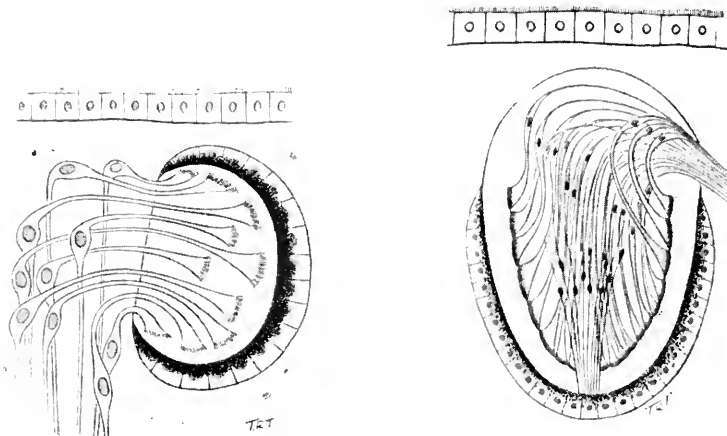


FIG. 92.—The eye of the turbellarian worm, *Planaria gonocephala*.

FIG. 93.—The eye of the nemertine worm, *Drepanophorus*.

epithelium and the elongated visual cells curve away from the surface to crowd into a cellular cup of densely pigmented cells. Such an organ in addition to being light-sensitive can appreciate the direction of incident light, and forms a primitive type of *directional eye*. A still more complicated organ of this type is seen in the paired eyes of Chaetognaths, such as the marine arrow-worm, *Spadella* (Hesse, 1902), and in the median eyes of certain Crustaceans.¹



Chaetognath

It is of interest that in this subepithelial type of eye the sensory pole of the cell is usually directed away from the incident light which has to traverse the cell-body in order to reach it ; technically, therefore, these are examples of an *inverted retina*.²

The Epithelial Invaginated Eye

A much more common arrangement, however, is an association of a number of contiguous cells in the epithelial layer, which as evolution progresses eventually invaginate into the underlying tissues. In such a development the first stage is the specialization of a number of con-

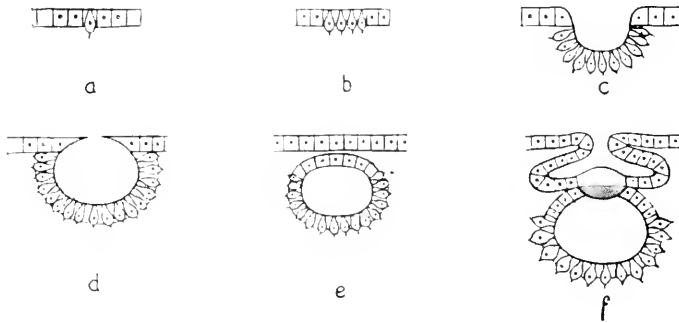


FIG. 94.—SCHEME OF DEVELOPMENT OF THE SIMPLE EPITHELIAL EYE OF INVERTEBRATES.

- (a) Single epithelial light-cell.
- (b) A group of light-cells forming a flat eye (Fig. 95).
- (c) The cupulate eye (Fig. 97).
- (d) The formation of a dark chamber (Fig. 100).
- (e) The vesicular eye (Fig. 110).
- (f) The eye of Cephalopods (Fig. 113).

tiguous surface cells to form a plaque on the surface—the FLAT EYE (Fig. 94b) ; the second stage is evident when the epithelium becomes invaginated so that the sentient cells line a simple depression on the surface—the CUPULATE EYE ; thus, while to some degree protected, their functional utility is increased by the crowding together of more units into the same space, and by an arrangement whereby they can orientate more accurately the incident light. A further improvement

¹ p. 152.

² p. 146.

is gained when the opening of the depression is narrowed so that a dark chamber with a pin-hole opening is formed. The last step in the differentiation of the simple eye is marked by the closure of the opening leading into the depression by a circular in-folding of the surrounding epithelium ; thus is formed the VESICULAR EYE, the highest differentiation of which is reached in the eye of Cephalopods wherein the vesicle is associated with a secondary invagination of the ectodermal layer which, in addition to providing a protective covering, helps to constitute a dioptric mechanism. The scheme of the development of the simple eye from its primitive beginning as a single cell to this highly complex structure is seen in Fig. 94.

The simplicity of these eyes is seen in their capacity for regeneration, a potentiality first demonstrated by Bonnet (1781). If the tentacle with the eye is removed from the edible snail or the grey slug, another regenerates, occasionally equipped with two eyes, a process which has been known to occur twenty times in succession (Galati-Mosella, 1915-17). Experimenting similarly on the gastropod, *Murex*, Carrière (1889) found that the regenerating eye initially took the form of a simple depression, which gradually closed leaving only a pore-like opening and eventually developed into a closed vesicle.

THE FLAT EYE

This is the most primitive association of light-sensitive cells and usually consists of 5 or 6 epithelial cells lying upon the surface, differentiated by being a little larger than their unspecialized neighbours. Such an ocellus is seen in the aquatic worm, *Stylaria lacustris*

FIGS. 95 AND 96 —FLAT EYES.

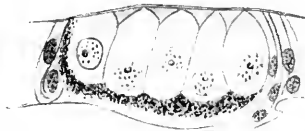


FIG. 95.—The ocellus of the aquatic annelid worm, *Stylaria lacustris* (after Hesse).

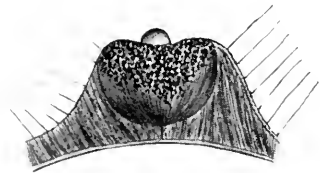


FIG. 96.—The ocellus of the hydromedusan, *Lizzia*, the epithelial sensory cells being capped by a lens-like thickening of the cuticle (Hertwig and Jourdan).



Dendrocaelum

(Fig. 95) (Hesse, 1908), in certain unsegmented planarian worms such as *Dendrocaelum* and some leeches, while in the larvæ of some insects the eyes consist merely of a pair of visual cells and two overlying pigment cells (Hesse, 1908 ; Imms, 1935). Occasionally a simple cuticular refringent apparatus is added to collect the light as well as pigment to absorb it ; thus in the hydromedusan, *Lizzia*, the eye, situated at the base of the tentacle, is composed of a number of sensory

cells associated with pigmented cells capped by a "lens" formed by a localized thickening of the cuticle (Fig. 96) (Hertwig, 1878 ; Jourdan, 1889).

THE CUPULATE EYE

The CUPULATE or CUP-SHAPED eye (*cupula*, a cup) forms a distinct functional advance, for the invagination of the light-sensitive epithelium allows the development of a primitive directional sense (Patten, 1886). Its development may be seen in three stages. The first is a simple

FIGS. 97-100.—TYPICAL CUPULATE EYES OF THE SIMPLEST TYPE.

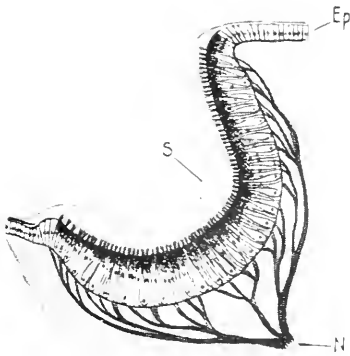


FIG. 97.—The ocellus of the limpet, *Patella*.

Ep, epithelium ; S, secretory substance covering visual cells ; N, nerve (after Hesse).



FIG. 98.—The ocellus of the ear-shell, *Haliotis*.

The cup-shaped depression is deep with a narrow neck and is filled with secretion formed by the epithelial cells (after Hesse).

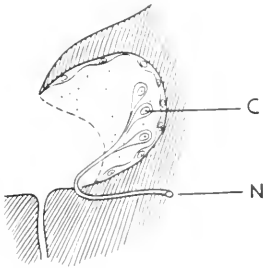


FIG. 99.—The visual organ of the larva of the house-fly, *Musca*.

There is a small cavity in the cephalo-pharyngeal skeleton wherein lie light-sensitive cells, C, from which issues the optic nerve, N (after Bolwig).

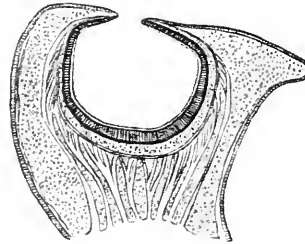
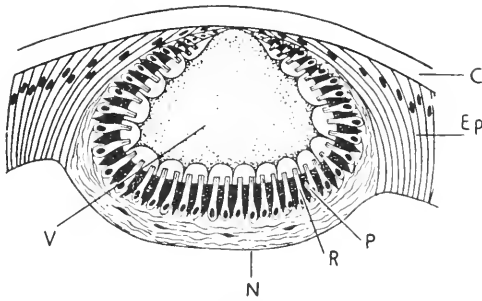
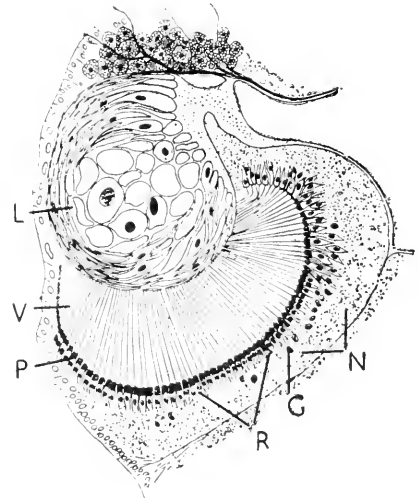


FIG. 100.—The ocellus of the mollusc, *Nautilus*, with its pin-hole opening (after Hesse).

FIGS. 101-3.—REPRESENTATIVE CUPULATE EYES OF A MORE COMPLEX TYPE.

FIG. 101.—The ocellus of the polychaete worm, *Nereis*.

C, cuticle ; Ep, epithelium ; N, nerve fibres ; P, pigment between the sensory cells ; R, nucleated sensory cells provided with cilia ; V, vitreous (after Hesse).

FIG. 102.—The ocellus of the Cubomedusan, *Charybdea*.

L, cellular lens ; V, "vitreous body" of the clear rhabdites of retinal cells ; P, pigmented zone of retinal cells ; R, retinal cells ; N, nerve tissue with ganglion cells, G (after Berger).

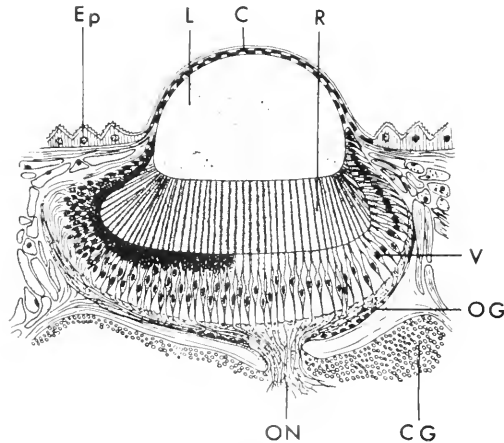
FIG. 103.—The eye of *Peripatus*.

FIG. 103.—Schematic sagittal section of the eye ; partly depigmented to demonstrate details of the visual cells.

C, cuticle ; CG, cerebral ganglion ; Ep, hypodermis ; L, lens ; OG, optic ganglion ; ON, optic nerve ; R, rods ; V, visual cells (after Dakin).

depression or dimple in the epithelium, such as is seen typically among Molluscs; some 30 such cup-shaped depressions, for example, each $\frac{1}{2}$ mm. in diameter, skirt the border of the mantle of the bivalve, *Lima*, while similar structures are seen at the base of the tentacles of the common limpet, *Patella* (Fig. 97). The simple eyes of the larva of the house-fly, *Musca*, are of a similar type (Bolwig, 1946) (Fig. 99).¹ In such cases the sensory epithelium may be composed of light-sensitive pigmented cells interspersed with unpigmented secretory cells which secrete a protective material covering the epithelium. The second stage is marked by an overlapping of the surface epithelium so that the shallow pit becomes converted into a cavity with a tiny opening. Such a cup may be oval and deep and filled with secretion, as in the ear-shell, *Haliotis* (Fig. 98), but the tendency is seen in its most marked form in the rare pearly mollusc, *Nautilus*, which lives in a beautiful spiral shell in the seas of the Far East (Fig. 100). In this cephalopod, situated just behind the tentacles, a pin-hole opening 2 mm. in diameter leads into a large ocular cavity lined by light-sensitive cells bathed by sea-water, the eye thus constituting a veritable dark chamber (Merton, 1905). In a third and final development the cavity is closed by the growth of the cuticle associated with hypodermal cells over the opening. Although a closed vesicle is thus formed, it is made up of the non-cellular cuticle which extends uninterruptedly over the cupula of the invaginated layer of cells, while the secretory mass elaborated by the sensory cells becomes enclosed to form a vitreous body (the marine polychaete worm, *Nereis*—Hesse, 1897–1908) (Fig. 101).

Once this stage has been reached, further advances can be made in the optical arrangements of such an eye. The simplest is the more or less elaborate thickening of the cuticular layer of the epithelium to form a refringent apparatus. In its most primitive form such an eye consists merely of a group of visual cells arranged in a hollow beneath a lens formed from the cuticle as is seen, for example, in the medusoid, *Sarsia*, or the louse, *Pediculus*, or other insects (Fig. 106). A somewhat similar morphology is seen in the eye of the Onychophore, *Peripatus*,² but in it the large lens is formed from the hypodermal cells and takes the place of the vitreous (Fig. 103) (Cuénot, 1949). Usually, however, hypodermal cells continuous, on the one hand, with the surface ectoderm and, on the other, with the sensory cells of the cupula, edge their way underneath the cuticle where they may form a clear, refractile mass underneath the cuticular lens constituting a primitive lens or vitreous (as in the ocelli of many insects and in some spiders, Figs. 104 and 105) (Bütschli, 1921; Wigglesworth, 1941; and others). Alternatively, as in the Cubomedusan, *Charybdea*, the distal ends of the retinal cells (rhabdites) develop greatly to form a clear

Larva of *Musca**Nautilus**Nereis**Sarsia**Pediculus**Peripatus*¹ p. 224.² p. 204.

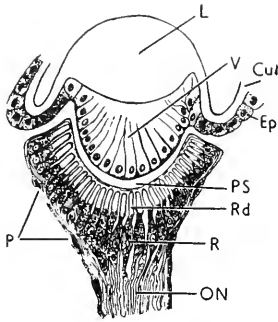


FIG. 104.—The frontal stemma of the imago of the blow-fly, *Calliphora* (after Lowne).

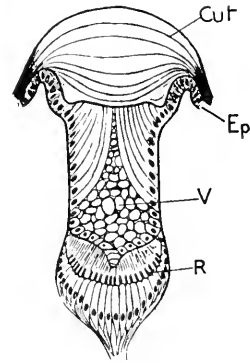


FIG. 105.—Sagittal section of the median anterior ocellus of the jumping spider, *Salticus* (after Bütschli).

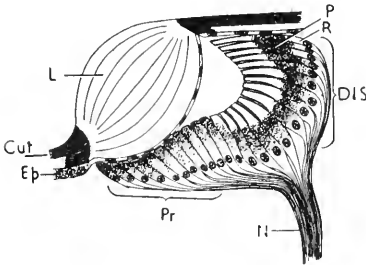


FIG. 106.—The frontal ocellus of the hover-fly, *Helophilus*.

DIS, cells with long sensory ends lying distant from the lens; Pr, cells with short sensory ends lying proximally to the lens (after Hesse).

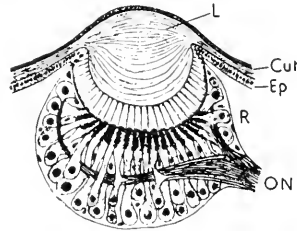


FIG. 107.—The anterior median ocellus of the house spider, *Tegenaria domestica*.

It is to be noted that the optic nerve fibres, ON, issue from the lateral aspect of the visual cells, R (compare p. 159).

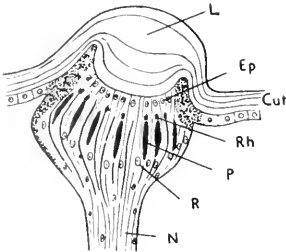


FIG. 108.—The dorsal ocellus of the insect, *Aphrophora spumaria* (after Link).

In Figs. 108-9 the eye is in every sense simple although there is some association of the visual cells around rhabdomes.

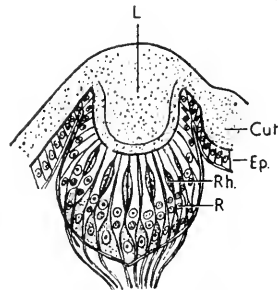


FIG. 109.—The lateral ocellus of the scorpion (after Lankester and Bourne).

Cut, cuticle; Ep, hypodermal epithelium; L, cuticular lens; N, ON, optic nerve fibres; P, pigment cells; PS, pretetinal space; R, retinal (visual) cells; Rd, rods or rhabdites; Rh, rhabdites; V, hypodermal cells forming vitreous.

“vitreous” mass (Fig. 102) (Berger, 1898; Berger and Conant, 1898–99). The lens may thus be acellular and cuticular, or cellular; the vitreous cellular or gelatinous, formed either as a secretion of the retinal cells or by their degeneration and coalescence.

An interesting modification is seen in the stemmata or simple eyes of the larval and pupal forms of some insects such as sawflies (Tenthredinidæ) and many beetles (Coleoptera) as well as in the ocelli of most adult insects, in the lateral eyes of the scorpion (Figs. 108–9), and the median eyes of the king-crab, *Limulus* (Fig. 142); in these the visual cells are arranged in loose groups of two or three around a rod-like structure secreted by the visual cells—the RHABDOME ($\rho\chi\beta\delta\omega\mu\alpha$, a rod). Such an arrangement does not alter the essential simplicity of the eye.

It has been suggested that some accommodative adjustment of a static type may be provided in these eyes by the existence of differences in the distance between the sensory cells and the lens (some flies, as *Helophilus*) (Fig. 106) (Hesse, 1908).



Helophilus

THE VESICULAR EYE

The final stage in the evolution of the simple eye is the closure of the invaginated epithelium to form an enclosed vesicle divorced entirely from the surface ectoderm and usually separated from it by mesenchyme. In its simplest form such an eye is merely a spherical vesicle lined with ectodermal cells; the cells of the proximal (deep) part of

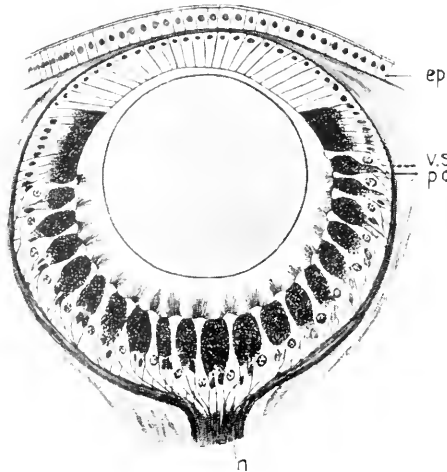


FIG. 110.—THE VESICULAR EYE.

The ocellus of the edible snail.

Ep, epithelium; vs, visual cell; pc, pigment cell; n, nerve (after Hesse).

*Buccinum**Helix*

the vesicle are partly light-sensitive, partly secretory, the former being frequently associated with pigment and connected by nerve fibres with the optic or cerebral ganglion; the distal (superficial) elements are relatively undifferentiated, and a refractile mass of secreted material, homologous with the vitreous of higher types, fills the cavity. Such a simple ocellus, lying in the subepithelial tissues over which the epithelium passes without interruption, is seen most particularly in Gastropods such as *Murex* which furnished the Tyrian purple,¹ the common whelk, *Buccinum*, or the edible snail, *Helix pomatia* (Fig. 110).

Its most elaborate form is seen in the spider- or scorpion-shell, *Pterocera lambis*, a gastropod found on tropical reefs, wherein the vesicle, filled with a vitreous-like material, has a clear distal wall (a cornea), while the proximal part

FIG. 111.—THE RETINA OF *PTEROCERA LAMBIS*.

The retina contains four layers: (a) a layer of rods; (b) a layer of pigment cells containing some rod nuclei; (c) a cellular layer in which are distinguishable most of the rod nuclei, bipolar cells, a few horizontal cells, ganglion cells and supporting cells with a reticulum resembling Müller's fibres in the vertebrate retina; (d) a layer of optic nerve fibres (J. H. Princee).

Shell of
Pterocera

of the vesicle is occupied by a retina consisting, according to Prince (1955), of 4 layers—(a) most distally, a layer of rod-like visual cells, (b) a layer of pigment cells, (c) a cellular layer containing the nuclei of the rods, synaptic "bipolar", "horizontal" and ganglion cells, and (d) a layer of optic nerve fibres, the axons of the ganglion cells which leave the eye in numerous optic nerve bundles (Figs. 111 and 189). With a receptor population approaching 10,000 per sq. mm., the sensitivity of the eye is probably considerable although, in the absence of an efficient optical system, image-formation must be very deficient.

In a further stage of complexity a lens is added to the vesicular eye so as to form a camera-like eye resembling that of vertebrates; an accommodative mechanism and an extra-ocular musculature are provided. This is typically seen in two very different phyla: among the Polychaetes in the family Alciopidae, and among the Cephalopods which have the most elaborate eyes in the invertebrate kingdom.

¹ Singer, *The Earliest Chemical Industry*, London, pp. 12-14 (1948).

The remarkable eyes of the Alciopidae, a family of pelagic polychaetes (*Alciopa*, *Vanadis*, etc.), have received considerable study¹ (Fig. 112). In these worms the proximal part of the vesicle is occupied by a retina with direct receptors; the main body of the vesicle contains a vitreous-like mass of two consistencies, separating the retina from the anteriorly situated lens. The posterior portion of the vitreous is jelly-like and is secreted by the intercalary cells of the retina; the distal portion is derived from a glandular cell situated ventrally. There is an effective accommodative mechanism² and the eyes are moved by 3 extrinsic muscles. Nothing is known about the function of these elaborate eyes.

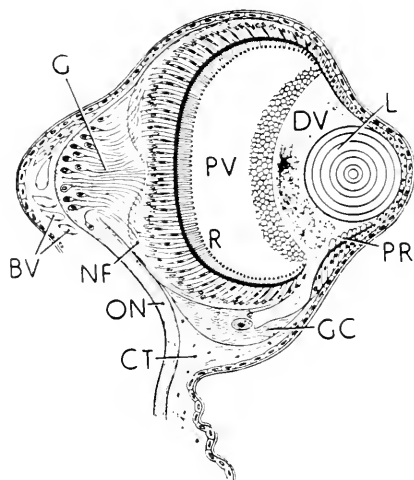


FIG. 112.—THE EYE OF THE POLYCHAETE WORM, *VANADIS*.

BV, blood vessels; CT, connective tissue; DV, distal vitreous; G, ganglion cells; GC, glandular cell secreting the distal vitreous; L, lens; ON, optic nerve; NF, optic nerve fibres; PR, proximal retina; PV, proximal vitreous; R, main retina showing the rods separated from the visual cell-bodies by a dense line of pigment (after Hesse).

The eyes of the dibranchiate cephalopods (cuttlefish, squids, octopus, etc.) have received a considerable amount of study (Figs. 113, 114).³ The two eyes are set on pedicles on either side of the head, and are partly enclosed in a dense supporting envelope reinforced with cartilage. The vesicle is filled with a vitreous secretion; the cells lining its proximal portion form the retina; the distal portion fuses with an invagination of the surface epithelium to form a composite spheroidal lens, the inner half of which is thus made up of vesicular epithelium, the superficial half of surface epithelium. On either side of the lens the fusion of these two layers forms a double epithelial layer—a "ciliary body"—and then the surface epithelium turns upon itself to form an "iris" before

¹ Greef, 1875-77; Demoll, 1909; v. Hess, 1918; Pflugfelder, 1932.

² p. 591.

³ See Scarpa (1789), Cuvier (1817), Soemmerring (1818), Kröhn (1835-42), Hensen (1865), Schultze (1869), Patten (1886), Carrière (1889), Grenacher (1895), Hesse (1900-2), Merton (1905), Bütschli (1921), Alexandrowicz (1927), Heidermanns (1928), and others.

THE EYE IN EVOLUTION

FIGS. 113 AND 114.—THE EYE OF A TYPICAL CEPHALOPOD.

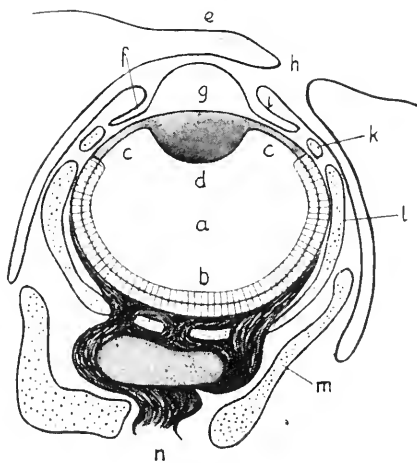
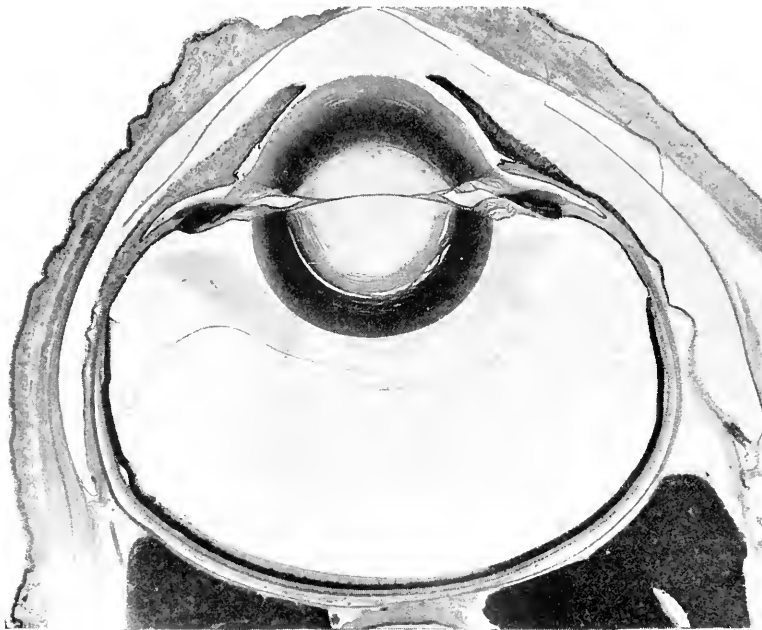


FIG. 113.

Invaginated epithelium forms the optic vesicle (*a*) lined by the retina (*b*), the posterior layer of the "ciliary body" (*c*), and the posterior part of the lens (*d*). The surface epithelium forms the cornea (*e*), the anterior part of the ciliary body (*f*), the iris (*i*), and the anterior part of the lens (*g*), a hole (*h*) being left at the point of invagination. The eye is surrounded by a cartilaginous orbit, formed by an anterior cartilage (*k*), an equatorial cartilage (*l*), and an orbital cartilage (*m*). *n* is the optic nerve.

FIG. 114.—The eye of *Octopus vulgaris* (specimen from J. Z. Young).

invaginating to line a voluminous cul-de-sac extending far posteriorly. Over this the transparent surface epithelium forms a "cornea", sometimes, in *Myopsidæ*, forming a continuous layer in which case the cul-de-sac (the "anterior chamber") is filled with an "aqueous humour" (cuttlefish, *Sepia* : squid, *Loligo*), sometimes, in *Ægopsidæ*, perforated by a hole so that the cavity is flushed by seawater (*Octopus*). The iris is supported by a plate of cartilage and both it and the ciliary body are provided with contractile muscular tissue. The pupil is rectangular in shape and actively contractile and there is an efficient accommodative mechanism¹ (v. Hess, 1909) : while covering the iris and extending some distance



Sepia

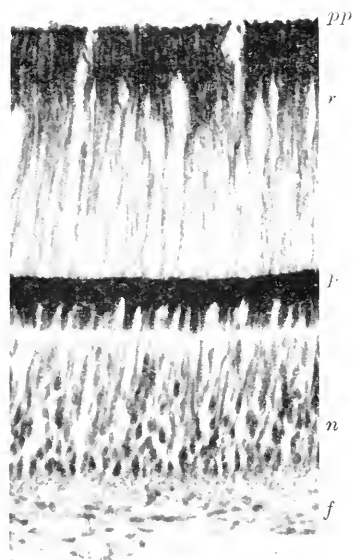


FIG. 115.—THE RETINA OF THE OCTOPUS.

The retina is composed primarily of a single layer of visual cells with rod-like terminations, *r*, and nuclei, *n*. Between the rods and the cell-bodies there is a dark line of pigment, *p*, and at the proximal extremities of the rods a layer of protective pigment, *pp*. Most externally there is a layer of nerve fibres, *f*, with ganglion cells. The white line underneath the pigment is an artefact at the site of a supporting membrane ($\times 150$) (from a specimen of J. Z. Young).

posteriorly, is a silvery membrane of pavement epithelium which glitters and shines like mother-of-pearl (Figs. 116–17 : Fig. 192).

The retina itself is comprised in the main of visual cells supported by two limiting membranes—an internal membrane lining the cavity of the vesicle and an external membrane dividing the retina transversely into two (Fig. 115). The visual cells are made up of two elements, a rod-like termination and a cell-body. The rods lie between the two membranes in palisade arrangement ; they are constricted as they pierce the external membrane, proximal to which lie the cell-bodies with their nuclei, the visual pathway being continued by nerve fibres running in an optic nerve to an optic ganglion.² Prince (1956) described



Loligo



Octopus

¹ p. 590.

² p. 528.

*Eledone*

bipolar cells and ganglion cells in the nuclear layer proximal to the pigmented layer. A considerable amount of pigment is found in association with the visual cells which is most abundant near the narrow neck of the cell between the rod and the cell-body, and in some species at any rate, it is claimed, migrates towards the extremities of the rods in bright light (*Eledone*—Rawitz, 1891).

Such an eye is thus a highly complex organ capable of image-formation and structurally equipped to mediate pattern-vision, able to accommodate over a considerable range and possessed of some power of adaptation. Indeed, in one species, *Bathyteuthis*, the elements of a central retinal area become apparent since

FIGS. 116 AND 117.—THE PUPILS OF CEPHALOPODS IN VARIOUS STAGES OF CONTRACTION.



FIG. 116.—The pupil of the octopus.



FIG. 117.—The pupil of the cuttlefish, *Sepia*.

the rods are greatly elongated as if to form a primitive area centralis, a differentiation suggesting the existence of a fixation mechanism endowed with considerable visual sensitivity (Chun, 1903).

The Inverted Retina

A peculiar form of simple eye is associated with an INVERTED (OR INVERSE) RETINA, that is, a retina wherein the visual cells are orientated so that their sensory ends are directed away from the incident light. As a rule, inversion of the retina is associated with a secondary invagination of the optic vesicle. In the usual form of VERTÉD (OR CONVERSE) RETINA, as we have seen, the cells lining the proximal (deep) portion of the vesicle form the visual cells and their orientation is quite straightforward; their receptive elements face the surface and the optic nerve fibres lead directly away from their proximal ends (Figs. 118, 120). In some cases, however, the cells lining the distal (superficial) portion of the vesicle form the visual cells; since the receptive elements face the interior of the vesicle, the light must traverse the cell-bodies before it reaches the end-organ, and the nerve fibres, issuing superficially, must

double backwards to reach the optic ganglion (Figs. 119–121). In such cases the proximal cells of the vesicle usually contain an absorbing pigment, and the receptive ends of the visual cells approximate closely to them, thus reducing the vesicle to a slit-like potential cavity. An arrangement which might at first sight seem anomalous thus acquires a distinct biological value. Moreover, in many species a reflecting crystalline layer, or TAPETUM, is found next to the receptive ends of the visual

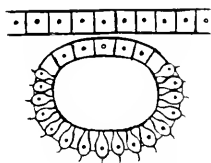


FIG. 118.—THE VERTED RETINA OF THE VESICULAR EYE.

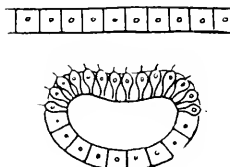


FIG. 119.—THE INVERTED RETINA OF THE VESICULAR EYE.

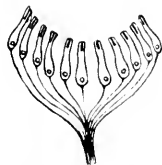


FIG. 120.—THE ARRANGEMENT OF THE VISUAL CELLS IN THE VERTED RETINA.



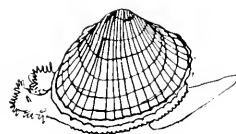
FIG. 121.—THE SIMPLEST ARRANGEMENT OF THE VISUAL CELLS IN THE INVERTED RETINA.

In each case light falls upon the visual cells from above (modified from Buxton, 1912).

cells which reflects the incident light backwards so that it traverses the sensory cells a second time thus doubling the intensity for stimulation and incidentally giving the eye a metallic sheen. This arrangement is therefore characteristic of animals to which vision in dim illuminations is important.

An inverted retina of this type is typical of Vertebrates but is rare among Invertebrates, being seen in a few Molluscs and Arachnids.

Among MOLLUSCS it is found in four species—in its simplest form in the pulmonate, *Onchidium*, and in the cockle, *Cardium*, and in its most elaborate form in two bivalves, the scallop, *Pecten*, and *Spondylus*. In the pulmonate mollusc, *Onchidium*, the visual cells of a simple vesicular eye are inverted and the optic fibres, issuing from their distal ends, pierce the posterior pole of the vesicle in a bundle exactly as does the optic nerve of Vertebrates (Fig. 122) (Semper, 1883). This peculiar eye is also unique in that the "vitreous" filling the optic cavity is made up of a small number of enormous cells. In *Cardium* the arrangement of the visual cells is somewhat similar but that of the optic nerve fibres



Cardium

completely different. The receptive ends of the visual cells lie upon an ectodermal layer of pigment cells crowned by a reflecting tapetum, while their distal ends are prolonged as nerve fibres which run over the retina towards the periphery and then bend backwards circumferentially to form the optic nerve which issues posteriorly.



Pecten

The eye of *Pecten* is of unusual interest (Fig. 123)¹; that of *Spondylus* is similar.² A single layer of epithelial cells forms the cornea, underneath this is a clear cellular lens, and posteriorly, separated from the lens by a transverse

FIGS. 122 AND 123.—INVERTED RETINÆ IN MOLLUSCS.

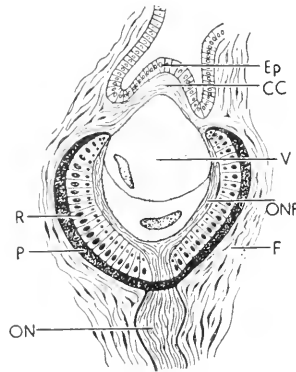


FIG. 122.—The dorsal eye of *Onchidium*. Showing an inverted retina pierced by the fibres of the optic nerve, resembling the arrangement in Vertebrates.

CC, connective tissue forming the cornea; Ep, epithelium; F, fibrous tissue capsule; ON, optic nerve; ONF, optic nerve fibres; P, pigment layer of the retina; R, visual cells of the retina; V, two large vitreous cells (after Gladstone).

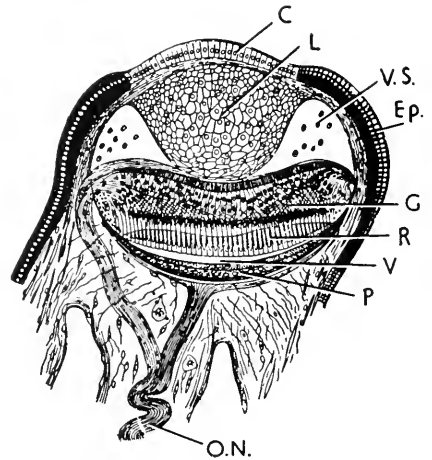


FIG. 123.—The eye of *Pecten*.

C, cornea; Ep, surface epithelium; G, ganglion cell layer of the retina; L, cellular lens; ON, optic nerve; P, layer of pigmented cells and above it, the tapetum; R, layer of rods; V, cavity of the vesicle; VS, vascular sinus (after Hesse).



Spondylus

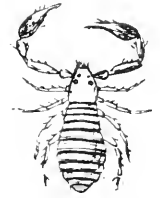
septum, lies the flattened optic vesicle, the cavity of which has become virtual. The retina itself is complicated. The proximal (deep) portion of the vesicle consists of a single layer of cubical pigmented cells covered by a tapetum; the more superficial portion of the vesicle consists of two well-defined layers—a proximal layer of rod-like visual elements, the receptive ends of which point posteriorly into the cavity of the vesicle, and a distal layer of cells (the ganglion cell layer of Patten, 1886) through which pass nerve fibres from the visual cells as they run towards the periphery at the equatorial region whence (as in *Cardium*) they encircle the posterior part of the globe to form the optic nerve (Küpfer,

¹ e. Keferstein (1862), Patten (1886), Kalide (1888), Carrière (1889), Schreiner (1890), Hesse (1900-2).

² Hickson (1882).

1915). It is interesting that in studying the electrical responses in the eye of *Pecten*, Hartline (1938) found that the distal layer of the retina mediated a strong off-response while the proximal layer discharged impulses whenever illuminated.

In ARACHNIDS, an inverse retina is seen in the lateral and median posterior eyes of spiders (Araneida). in all the ocelli of pseudo-scorpions (Pseudoscorpionidea). in the lateral eyes of whip-tailed scorpions (Pedipalpi) and in sea-spiders (Pycnogonida). Each one of these has a



Pseudo-scorpion

FIGS. 124 TO 127.—INVERTED AND SEMI-INVERTED RETINÆ IN ARACHNIDS.

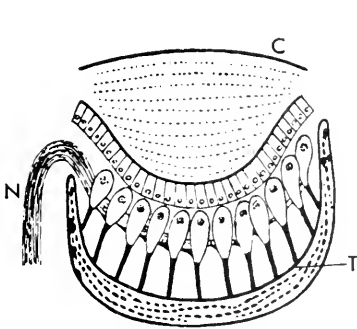


FIG. 124.—The lateral eye of a whip-tailed scorpion.

C, euticular lens; N, optic nerve fibres; T, tapetum (after Versluys and Demoll).

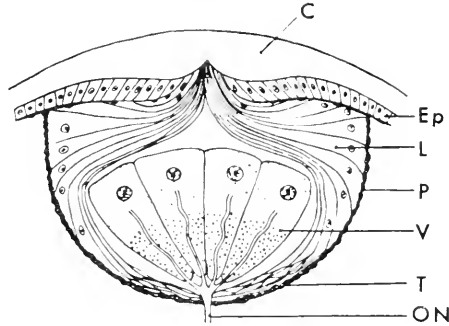


FIG. 125.—The eye of a sea-spider.

C, euticle; Ep, the hypodermal cells, the central ones of which become extremely elongated and surround the retinal cells, V. In the distal part of the eye they give rise to the cells of the lens, L, and in the proximal part, to the tapetum, T. The retinal cells themselves are elongated with a nucleus in the distal part, while the proximal granular part is the sensory receptor. Into these cells the optic nerve fibrils, ON, ramify. The whole eye is surrounded in a pigment capsule, P (after Schlottke).

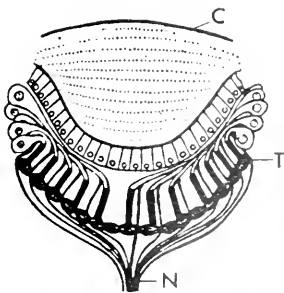


FIG. 126.—The lateral eye of a spider.

C, euticular lens; N, optic nerve fibres; T, tapetum (after Versluys and Demoll).

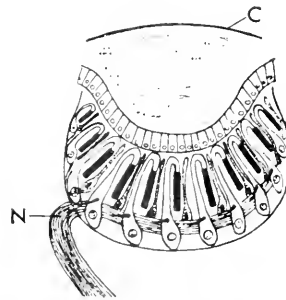


FIG. 127.—The median eye of a whip-tailed scorpion.

C, euticular lens; N, optic nerve fibres (after Versluys and Demoll).



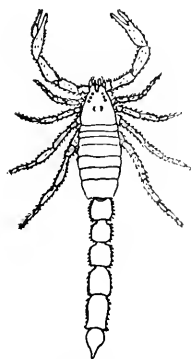
Whip-scorpion



Sea-spider



Web spider



Scorpion

different arrangement. In a further variation, seen in the median eyes of scorpions (Scorpionidea) and in the median eyes of whip-tailed scorpions, the visual cells are doubled upon themselves so that the base of the cell is verted and the sensory end inverted.

The simplest arrangement of an inverted retina in Arachnids is seen in the lateral eyes of whip-tailed scorpions (Fig. 124); the sensory ends of the inverted visual cells rest on the tapetum, directed away from the incident light, and from the mid-point of the cell-bodies the nerve fibres emerge to run to the periphery whence the optic nerve emerges on the side of the eye (Versluys and Demoll, 1923).

A different arrangement again is found in the sea-spiders (Pycnogonids) (Fig. 125). In these, the hypodermal cells secrete a cuticular lens in the anterior part of the eye and a reflecting tapetum in the posterior part. The visual cells are unusually interesting. They are large and triangular in shape, the apex of the triangle lying on the tapetum; the nuclei are placed distally at the base of the triangle and the narrow proximal ends filled with granular material form the receptive portion of the cell. The arrangement of the optic nerve fibres is unique for they interweave in the substance of the large retinal cells, reaching distally towards the nuclei.¹

An ingenious arrangement which probably has optical advantages is seen in the lateral and posterior median eyes of web-spiders: the (anterior) median eyes of these animals have direct, verted retinae (Widmann, 1908). In the former the sensory portions of the elongated visual cells point proximally to lie on the tapetum, while the cell-bodies are bent on themselves at an angle of 90° , to run towards the periphery of the retina where the nuclei lie (Fig. 126); this portion of the cell does not therefore interpose itself in the path of incident light (Versluys and Demoll, 1923).

A *semi-inverted retina* is found in the median eyes both of scorpions and of whip-scorpions. Here the visual cells, grouped in retinules around rhabdomes, are bent upon themselves at 180° , their nuclei lying proximally next to the tapetum and the receptor ends of the cells being bent round so that their extremities lie alongside the nuclei: here again there is the optical advantage that the incident light does not travel through the bases of the visual cells (Fig. 127) (Scheuring, 1913; Versluys and Demoll, 1923).

It will be remembered that the subepithelial eyes seen most typically in polychaetan and nemertine worms² wherein the visual cells dip downwards from

¹ Morgan (1891), Korschelt and Heider (1893), Bouvier (1913), Wiren (1918), Schmitt (1933).

² Ibid. 1934.

the surface into a cup of pigmented cells, and the conducting prolongations of the cells are turned towards the direction of the incident light, have the configuration of an "inverted" retina. In a sense, also, the composite simple eyes of Chætognaths and some of the smaller Crustaceans to be discussed immediately are also of this type.

AGGREGATE EYES

The AGGREGATE EYE is a suitable name to designate an accumulation of ocelli so closely packed that they bear a superficial resemblance to a compound eye although each is anatomically separate. Such an arrangement is seen in its most simple form in starfishes (Plate I), in such insects as the male *Stylops*¹ or in Myriapods (Fig. 210),² in which it appears as a cluster of ocelli.

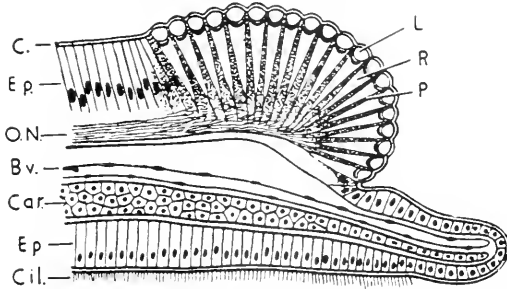
*Stylops*FIGS. 128 AND 129. THE AGGREGATE EYE OF *BRANCHIOMMA VESICULOSUM*.

FIG. 128.—Cross-section through a branchial filament of the worm.

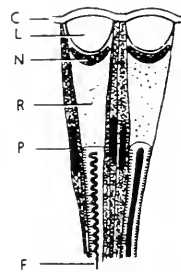
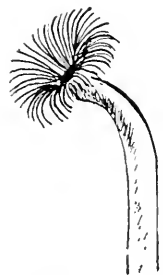


FIG. 129.—Axial section through two ocelli.

BV, blood vessel; C, cuticle; Car, cartilage; Cil, cilia; Ep, epidermis; F, fibril; L, lens; N, nucleus; ON, optic nerve; P, pigment cells; R, visual cell (after Hesse).

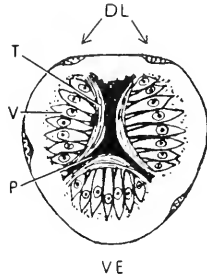
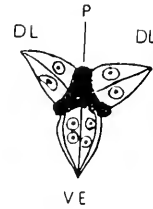
An entirely different type of aggregate eye is seen in the branchial filaments of some sedentary polychæte worms and in certain lamelli-branch molluscs wherein the organ has a superficial structural resemblance to a compound eye but each element contains only one sensory cell (Figs. 175-6). In the first case, the eye of the polychæte, *Branchiomma vesiculosum*, is made up of a spherical group of elements resembling ommatidia, but since each contains only a single cell it should be considered an ocellus and the eye is technically a simple organ of the aggregate type (Brunotte, 1888; Hesse, 1896-99) (Figs. 128 and 129). It is to be remembered, however, that in such tube-worms these structures do not seem to be essential for the animal's characteristic response to changes in light intensity (Millott, 1957). A similar arrangement is seen in the eyes of the lamelli-branch molluscs, *Arca* and *Pectunculus* (Carrière, 1885; Patten, 1886; Hesse, 1900).

*Branchiomma*¹ p. 221.² p. 210.

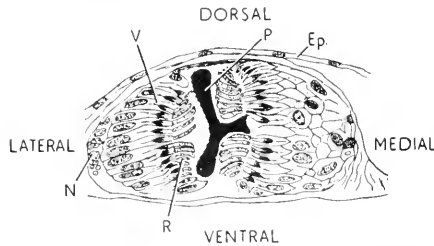
COMPOSITE OCELLI

COMPOSITE OCELLI (SIMPLE EYES) are formed by the fusion of two or more ocelli each with its own retina and pigment cup, a process which seems to have arisen independently in several phyla ; in

FIGS. 130 TO 132.—THE COMPOSITE OCELLUS.

FIG. 130.—The ocellus of *Cypris*.FIG. 131.—The ocellus of *Daphnia*.

The unpaired median eye represents the fusion of 3 ocelli (see Fig. 228). DL, dorso-lateral ocelli ; VE, ventral ocellus ; P, pigment mantle ; V, visual cells ; T, tapetum (after Claus, 1891).

FIG. 132.—The ocellus of the chaetognath, *Spadella exaptera*.

Showing 3 of the 5 simple eyes, one to the left and 2 to the right, arranged round the central pigment. P, Ep, epithelium ; V, visual cells ; R, rods ; N, nerve fibres (after Hesse).

*Cypris**Cyclops*

general, the fusion is associated with degeneracy and lack of use. It is interesting that the same cyclopic tendency is seen in the median (pineal) eye of Vertebrates, which initially was a paired organ.¹ Among certain smaller Crustaceans, lowly types which have undergone much reduction of the head and have largely lost their segmentation, a median unpaired eye is a characteristic feature, and is frequently composed of the fusion of a number of ocelli arranged in a somewhat similar way (the Cladoceran, *Daphnia* ; the Ostracods, *Cypris* and *Cypridina* ; the Copepod, *Cyclops*) (Figs. 130 and 131).² Among the marine arrow-worms (Chaetognatha), *Spadella* has two composite ocelli near the anterior extremity of its body, each organ made up of the fusion of 5 simple eyes of the cupulate type arranged around a central

¹ p. 711.² p. 163, Fig. 145.

mass of pigment which sends out partitions between each (Fig. 132) (Hesse, 1908). In such eyes the receptor ends of the sensory cells are directed inwards towards the cup of pigment, and the nerve fibre is peripheral so that the eye may be considered as of the inverted type (Vaissière, 1955).

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Joh. Müller Prof.

FIG. 133.—JOHANNES MÜLLER (1801-1858).

The Compound Eye

Nothing could be more suitable to introduce this section on the anatomy and physiology of the compound eye than the portrait of JOHANNES MÜLLER (1801-1858) (Fig. 133), Professor of Physiology first at Bonn and then at Berlin, a student, friend and collaborator of von Helmholtz. In association with Malpighi and Haller, he may be considered the founder of the great German School of Biology of the 19th century. Throughout his relatively short

career he contributed lavishly to many branches of biology but perhaps the conception for which he is best remembered is the *law of specific nerve energies* which lays down that each organ, however stimulated, gives rise to its own characteristic sensation.¹ His enunciation of the Mosaic Theory to explain the optical properties of the compound eye has stood the test of time, and was the first scientific explanation advanced on this subject ; Fig. 156 is a characteristic illustration from his book. His classical textbook on human physiology² crystallized the knowledge of his day in a vast compendium which stimulated work in every field for more than one generation.

The compound eye, an organ peculiar to Arthropods, has evolved along different lines from the ocellus. In the former, instead of being independent of each other, *the sensory elements are structurally and functionally associated in groups*. For this purpose complexity has been attained by the division of the individual sensory cells of a simple

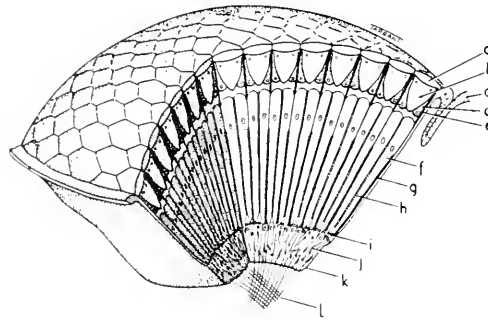


FIG. 134.—THE COMPOUND EYE.

Diagram of a compound eye of an insect with a sector excised.

a, corneal facet ; *b*, crystalline cone ; *c*, surface epithelium ; *d*, matrix cells of cornea ; *e*, iris pigment cell ; *f*, cell of retinule ; *g*, retinal pigment cell ; *h*, rhabdome ; *i*, fenestrated basement membrane ; *j*, nerves from retinular cells ; *k*, lamina ganglionaris ; *l*, outer chiasma.

eye to form a coordinated colony, a process first shown to occur in the development of the stalked eyes of the shrimp, *Crangon*, by Kingsley (1886) and confirmed by others in many different species. Moreover, optical imagery has been attained not by the single large lens characteristic of the ocellus (or of the vertebrate eye) which by attaining an adjusting mechanism reached its highest development in Cephalopods, but by ensheathing each individual group with pigment, thus converting the eye into a series of blackened tubes so that the multiplicity of images increases the acuity of vision by a mosaic effect. In this arrangement each separate element is called an *OMMATIDIUM* ($\delta\mu\mu\alpha$,

¹ *Zur vergleichenden Physiologie der Gesichtssinnes*, Leipzig, 1826.

² *Handbuch der Physiologie der Menschen*, 1834 40, translated into English in Baly's *Elements of Physiology*, London, 1838-42.

eye ; dim. $\delta\mu\mu\alpha\tau\acute{\iota}\delta\iota\omicron\nu$) ; the typical formation of the whole eye is seen in Figs. 134 and 150.

The development of ocelli and compound eyes indicates their essential kinship despite their outward disparity of form. The ocellus, as we have seen, originates as a hypodermal pit, the superficial cells of which, infolding under the cuticle, become differentiated into a refringent apparatus, the deeper cells into the retinal elements. Each ommatidium of the compound eye originates somewhat similarly as a consolidated pillar of hypodermal cells and between the pillars lie undifferentiated cells (Fig. 135) ; the superficial cells of these pillars form the basis of the corneal facets, the crystalline cones and primary pigmented cells, the deeper cells develop into the retinules, while those between the pillars form the secondary pigmented cells. In both cases the basement membrane is continuous with that of the integument (Patten, 1888-1912 ; Johansen, 1893 ;

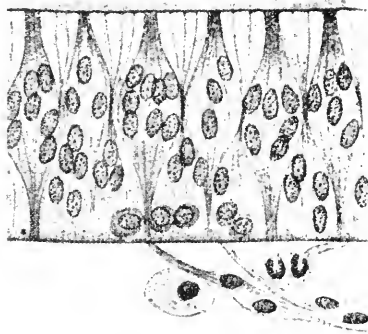


FIG. 135.—THE DEVELOPMENT OF THE COMPOUND EYE.

An early stage in the development of the eye of the pupa of the moth, *Saturnia pernyi*, showing the ommatidial pillars (after Bugnion and Popoff).

Bugnion and Popoff, 1914). It would thus seem that ontogenetically as well as phylogenetically the two types of eye are parallel developments from some (unknown) common primitive origin.

While ocelli and compound eyes show this kinship in development, the studies of Watake (1890) and Hanström (1926) would indicate that they have a different origin : all true compound eyes arise from the lateral ectodermal mass in the embryo, while ocelli take origin from either the dorsal or the ventral ectodermal mass. Although the lateral ocelli of modern arachnids and all the eyes of diplopods and chilopods arise from the lateral mass, Hanström considers them to represent degenerate forms of the ommatidia of compound eyes.

It would thus seem reasonable to assume that the compound eye has evolved from the simple eye at an early period, but it is clear that the first is not an adaptive modification of the second after it has reached an elaborate stage of development. It is true that intermediate stages are extant—the association of the sensory cells into a group under a single common lens, seen in the simple ommatidium of some larval and adult insects and Copepods (Fig. 138), or the multitubular arrangement of the aggregate eye wherein each element contains a single sensory cell, seen in some polychaete worms (Fig. 128). It is significant,

however, that among the earliest fossils known to man—the Trilobites, Arthropods which crept over the ooze of the sea-bed, and the Eurypterids, enormous marine spider-like creatures sometimes over 6 feet in length, which flourished in the Palæozoic era more than 300 million years ago and are long since extinct—both median ocelli and lateral compound eyes are present which have reached a high stage of complexity (Figs. 136 and 137) (Brink, 1951). It would seem, therefore, that both types of eye were derived from a simple ancestral stock

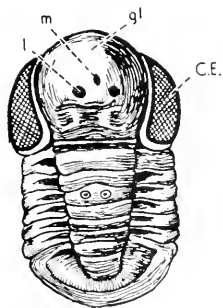


FIG. 136.—RECONSTRUCTION OF THE FOSSIL TRILOBITE, *ÆOLINA PRISCA*.

On the glabella (*gl*) there are impressions of a median, *m*, and paired lateral ocelli, *l*. The compound eyes, *C.E.*, are very large (after Barrande).

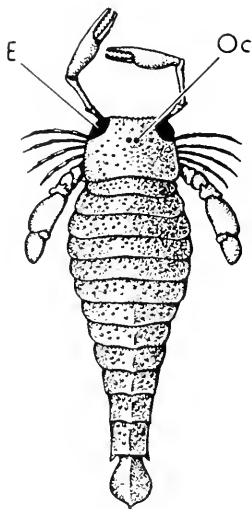


FIG. 137.—RECONSTRUCTION OF THE FOSSIL EURYPTERID, *PTERYGOTUS ANGLICUS*.

An ancient extinct Arachnid found in the Old Red Sandstone rocks in Scotland. It is possessed of elaborate compound eyes, *E*, as well as two dorsal ocelli, *Oc*.

before the beginning of known geological time, that each has evolved in its different way along diverging lines, and that their general form as seen today has been essentially the same since the early Palæozoic period.¹

The Structure of the Compound Eye

The essential structure of each ommatidium is relatively simple. Most superficially the cuticle forms a CORNEAL FACET (Fig. 134) underneath lies the CRYSTALLINE CONE, usually with two convex surfaces, the two together acting as a light-collecting system. The remainder of the organ is occupied by the sentient elements arranged in tubular form: this associated group of cells is called the RETINULE the cells of which rest upon a fenestrated basement membrane and are arranged so that their differentiated inner borders together form a

¹ Compare p. 754.

central refractile rod, the RHABDOME. The rhabdome is a product of the collective secretion of the cells of the retinule and has a light-conducting function; presumably in its substance photochemical changes occur, the products of which stimulate the neighbouring reticular cells, but the nature of the absorbing pigments has not yet been elucidated. The entire group of ommatidia, each individual of which is separated in some degree from its neighbour by a mantle of pigment cells, constitutes the compound eye, the surface being made up of the corneal facets fitting into each other to form a mosaic (hence the common name "faceted" eye), and the retinules together forming the retina. The structure would therefore suggest that light striking a retinule stimulates it as a whole and produces a single sensation, and consequently the great advance in the development of the compound eye is the coordination of individual elements in a unity of function. The mosaic of vision is made up of the images from the individual ommatidia of which there may be few or many, each of which acts in the same way as a single retinal cell of the simple eye. As in the ocellus, the entire structure is derived from the surface ectoderm.

The sensory mechanism of the compound eye is not at all clear for on this subject much research yet remains to be done. Most authorities accept that the reticular cells are the photosensitive elements¹; these form a characteristic complex for any given species and are precisely arranged, usually 7 or 8 in number but varying from 4 to 20 in different species of Arthropods. It used to be generally accepted that each reticular cell was a primary neurone, and certainly each extends proximally as an axon which terminates synaptically in optic ganglia or nuclei; but the interesting thing is that on the few occasions in which the matter has been experimentally explored, no conducted action potentials have ever been demonstrated in these cells or their axons (Bernhard, 1942; Autrum and Gallwitz, 1951). In the king-crab, *Limulus*, it has long been known that only one active fibre can be detected in the whole bundle of axons emerging proximally from the retinule (Hartline and Graham, 1932; Hartline *et al.*, 1952-53), and Waterman and Wiersma (1954) have brought forward significant evidence that this activity is associated with a characteristic eccentric cell one of which is found in each ommatidium. In Crustaceans little work has been done germane to this problem, but it would seem that the electronic spread of retinal potential travels towards the first optic ganglion without giving rise to any spikes (Hanaoka, 1950). In these and in Insects the conducting neurones may be located in the first optic ganglion (the lamina ganglionaris)² which lies immediately under the basement membrane of the retina. In Insects there are also units comparable to the eccentric cells of *Limulus*, the axons of which do not terminate with those from the reticular cells in the first optic ganglion but in the next more proximal ganglion (Cajal and Sanchez, 1915; Hanström, 1927). The evidence available to-day would, indeed, suggest the somewhat surprising deduction that although the photosensitive region is near the rhabdomes of the

¹ According to Berger and Courrier (1952) the photoreceptors in the eyes of Insects are situated at the bases of the rhabdomes and are not represented by the longitudinal cells usually designated as "sensory".

² p. 52.

reticular cells, the axons of these cells do not conduct impulses even although they form the majority of the fibres of the optic nerve, while this function is taken over by other structures analogous to the bipolar cells of the vertebrate retina, the electronic potentials induced by the primary receptor process giving rise to propagated impulses in closely contiguous conducting neurones. It is obvious that many fascinating problems still remain to be elucidated.

As in other evolutionary processes it cannot be said that a cut-and-dried differentiation exists between the simple and the compound

eye. Intermediate forms between the two may be seen in some worms. On the one hand, as we have already seen,¹ some sedentary polychæte worms and lamellibranch molluscs are provided with structures superficially resembling a compound eye, but since each element contains a single visual cell they are more correctly termed AGGREGATE EYES. On the other hand, the stemmata of the larvæ of most holometabolous insects and the lateral ocelli of many adult types such as butterflies and moths (Lepidoptera) and all the ocelli of springtails (Collembola) have structures somewhat resembling the single ommatidium of a compound eye, consisting of a cornea, a crystalline lens and seven reticular cells arranged around a central rhabdome (Dethier, 1942-43; and others); such an arrangement may be called a SIMPLE OMMATIDIAL EYE (Fig. 138). The ventral eye of Copepods forms a similar intermediate step between an ocellus and an ommatidium.

FIG. 138.—THE SIMPLE OMMATIDIAL EYE OF THE LARVA OF THE MOTH, *GASTROPACHA RUBI*.

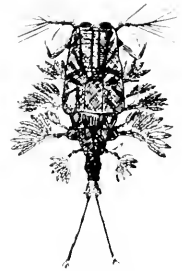
A lens and retinule are arranged after the manner of a single ommatidium (after Demoll).

C, corneal lens; Ep, epithelial cell; L, lens; M, mantle cell; R, R, visual cells; Rh, rhabdome; V, vitrellæ.

Thus the female *Pontellopsis regalis*, for example, has an eye composed of a single retinule of 6 cells arranged in two groups of 3 (Vaissière, 1954), while *Copilia* and its relatives have a single group of 3 cells arranged around a rhabdome (Grenacher, 1879-80; Exner, 1891).

These tiny crustaceans have unique eyes (Fig. 139); each is almost half as long as the body and is pulled about in all directions with great rapidity by muscles, a device presumably designed to increase its visual field. Moreover, the optic nerve issues, not from the proximal end of the ommatidium, but from its side. A similar point of exit for the optic nerve from the middle of the lateral wall of the visual cells is seen in the anterior median ocelli of the common house spider, *Tegenaria domestica* (Bütschli, 1921) (Fig. 107).

True compound eyes, however, are seen only among the Arthropods. They occur in several fossil forms (Trilobites, Eurypterids,



Copilia



Tegenaria

*Scutigera**Phronima**Dineutus**Stylocheiron*

Chilopods and Diplopods), in the centipede, *Scutigera*, and its close allies; in Arachnids an atypical form occurs in the lateral eyes of the king-crab, but their full development is characteristic of Crustaceans and Insects, in which they are found in the most varied forms. Of these, the most elaborate are the COMPOSITE COMPOUND EYE wherein the organ is formed by the apparent fusion of two compound eyes, usually a frontal and a lateral. Among Crustaceans this is seen in pelagic Schizopods (Hesse, 1908), or in some Amphipods such as *Phronima sedentaria* (Claus, 1879). Among Insects a frontal and lateral combination is seen in some flies (Diptera) and mayflies (Ephemeroptera), a dorsal and ventral in wasps (Vespoidea) and longhorn beetles (Cerambycidae) (Fig. 140). Such an arrangement undoubtedly increases the visual field and may also serve as an accommodative device providing two focusing mechanisms, one anatomically adjusted for distant and the other for near vision (Dietrich, 1909; Weber, 1934). A further example is the dorsal and ventral eyes of the whirligig beetle, *Dineutus*, the former for aerial vision and the latter for vision under water (Fig. 231).

A final complication is seen in some abyssal Crustaceans wherein a frontal portion of the compound eye contains few ommatidia provided with little pigment, obviously adapted for dim light, a lateral portion has many small ommatidia each of which is ensheathed in pigment so as to be effective in brighter light, while immediately below this a third part is adapted as a luminous organ¹ (*Stylocheiron mastigophorum*—Chun, 1896) (Fig. 141).

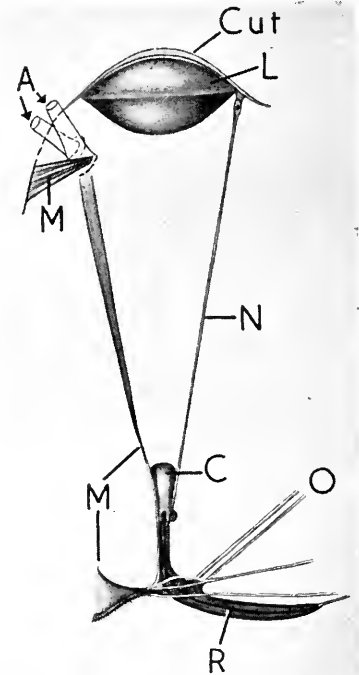


FIG. 139.—THE EYE OF THE COPEPOD, *COPILIA* (FORESHORTENED).

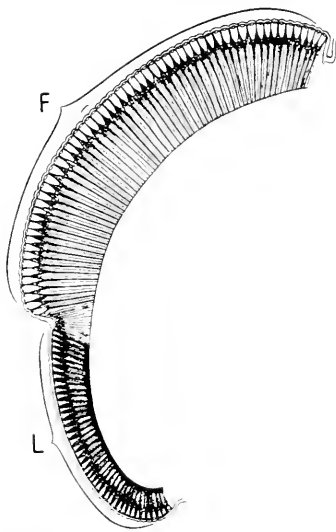
Cut, cuticle; L, lens; N, nerve fibre to epidermis; C, crystalline cone; O, optic nerve; R, rhabdome with surrounding sensory cells, encased in a pigment mantle; M, muscle; A, antennae (after Grenacher).

THE COMPOUND EYES OF ARACHNIDS

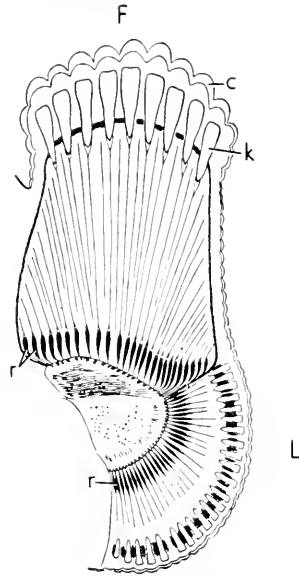
In general Arachnids are provided with ocelli, but in a few cases—the scorpion, the median eyes of the whip-scorpion and of the king-crab—the eye is of the type wherein the visual cells are arranged in groups,

¹ p. 736.

FIGS. 140 AND 141.—THE COMPOSITE COMPOUND EYE.

FIG. 140.—Frontal section of the eye of the male April fly, *Bibio marci*.

F, frontal eye ; L, lateral eye (after Hesse).

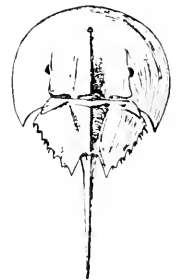
FIG. 141.—The faceted eye of the Schizopod, *Stygocheiron mastigophorum*.

F, frontal eye ; L, lateral eye ; c, corneal lens ; k, crystalline cone ; r, rhabdome. The luminous organ is not shown (after Hesse).

each around a rhabdome, the whole collection lying underneath a common lens (Fig. 142). The large lateral eyes of the king-crab, however, are unique and merit a special description.

The compound (lateral) eyes of the king-crab, *Limulus*, are of a relatively simple but unique structure, but are of unusual interest since they have been widely used by Hartline and his collaborators as a means of studying the electrical activity of photoreceptor cells ; their choice was determined by the fact that one fibre only of the optic nerve apparently acts as a conductor on stimulation of an ommatidium. A considerable amount of work has been done on the minute structure of this eye, but some points in the anatomy, particularly of its nervous connections, still remain obscure¹ (Fig. 143).

Although the eye shows wide differences in size and complexity of structure with growth and between species (Waterman, 1954), as a rule it consists of some 600 ommatidia, the whole being covered with a continuous corneal stratum of transparent chitin ; on its inner surface this presents a series of papilliform downgrowths which act as corneal lenses to the barrel-shaped retinules which

*Limulus*

¹ See Lankester and Bourne (1883), Watase (1890), Miller (1952), Waterman and Wiersma (1954).

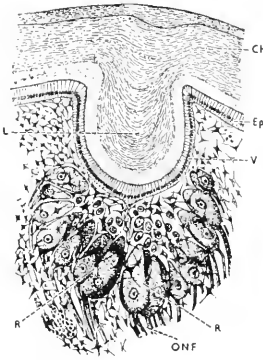
FIGS. 142 TO 144.—THE EYES OF THE KING-CRAB, *LIMULUS POLYPHEMUS*.

FIG. 142.—The median eye.

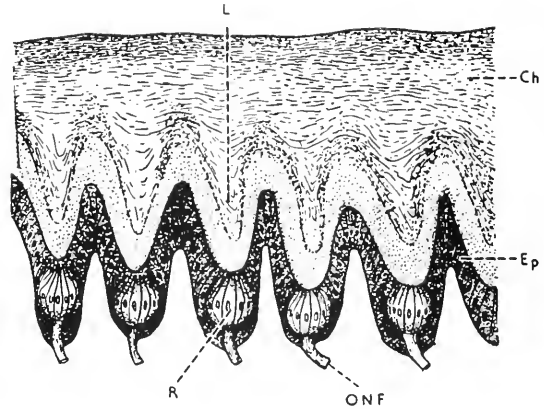


FIG. 143.—The lateral eye.

Ch, chitinous carapace, with the papilla-like thickening forming a lens, L ; Ep, hypodermal epithelial cells ; ONF, optic nerve fibres ; R, retinal cells ; V, continuation of the hypodermal cells to form a vitreous lamina (after Lankester and Bourne).

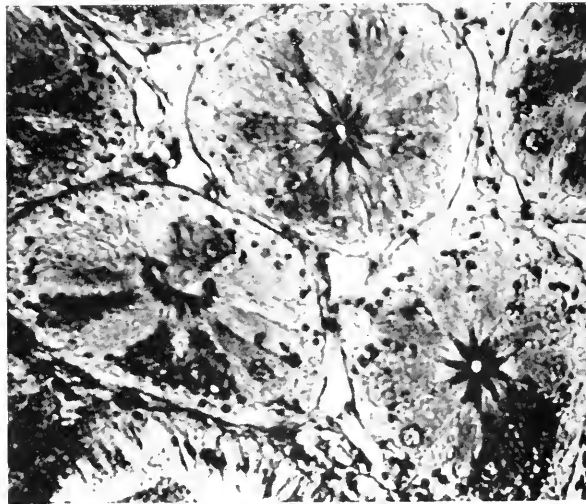


FIG. 144.—Section of the lateral eye.

Tangential section through the retina. The top ommatidium is cut perpendicular to the longitudinal optic axis. Each retinule consists of a cluster of cells (10 to 15 in number) arranged round the darkly staining, star-shaped rhabdome. The left-central ommatidium was sliced obliquely and more proximally and shows the body of the eccentric cell running into the axial canal of the central rhabdome towards 1 o'clock (Waterman and Wiersma, *J. exp. Zool.*).

lie directly beneath them. The retinule contains two types of cell. The main mass is made up of about a dozen elongated sensory cells grouped round central rhabdomes, their prolongations giving rise to fibres which mingle in a plexus before they emerge to run proximally in the optic nerve (Fig. 144). In each retinule there is also one eccentric cell the axon of which travels down the central rhabdome and along the nerve; it would seem probable that this forms the conducting element for nerve impulses set up by stimulation of the retinular cells (Hartline *et al.*, 1953; Waterman and Wiersma, 1954).¹ A white pigmented structure, the *rudimentary eye*, lies behind the posterior margin of the compound eye and sends a third type of large nerve fibre into the optic nerve (Waterman, 1950; Waterman and Enami, 1953).

THE COMPOUND EYES OF CRUSTACEANS

Crustaceans show two types of compound eyes—a relatively primitive type associated with the smaller species and a well formed type associated with the larger (crayfish, lobster, crab, etc.).

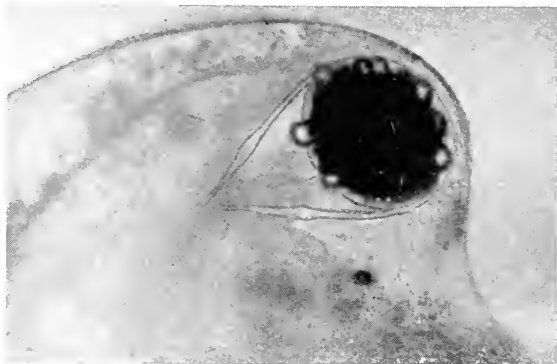


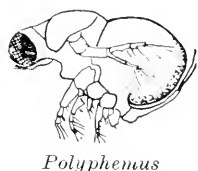
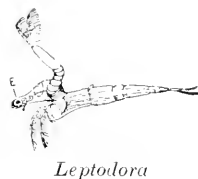
FIG. 145.—THE HEAD OF THE WATER-FLEA, *DAPHNIA*.

The compound eye is seen above with several of its 22 ommatidia appearing as rounded facets in a bed of pigment. Two of the 4 ocular muscles are also seen encircling the eye.

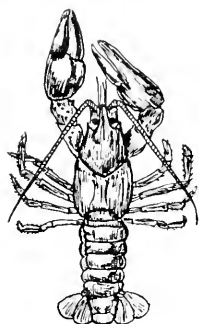
Underneath, the pigmented spot is the composite ocellus which lies in the mid-line; it is made up of the fusion of 3 ocelli (E. F. Fincham) (see Fig. 131).

The compound eyes of the tiny Branchiopods and some Ostracods are relatively primitive organs with poorly formed ommatidia. The compound eye of the water-flea, *Daphnia*, may be taken as representative (Fig. 145). It is composed of 22 rudimentary ommatidia arranged in a sphere of pigment and represents the fusion of two lateral eyes. The eyes of other Branchiopods are often more elaborate, *Leptodora*, for example, having 300 facets and *Polyphemus* 160. In those Ostracods which possess compound eyes, the organs are sometimes separate (paired) if the median composite ocellus is present, but fused if the latter is lacking. On the average they possess between 4 and 50 ommatidia (Cypridine, etc.).

The compound eyes of Malacostraca consist of ommatidia built upon the standard plan of a cuticular cornea, a crystalline cone, and a



¹ p. 158.

*Astacus*

retinule, the whole being more or less encased by pigmentary cells. As a general rule the ommatidia are fewer than in the eyes of Insects, but many variations in detail exist¹; a typical example is seen in Fig. 146 which illustrates the eye of the crayfish, *Astacus*. The cuticular cornea is not invariably faceted as is usually the case in Insects, but, for example, in Amphipods appears as a flat extension of the cuticle of the integument. Underneath the cuticle is invaginated a layer of hypodermal cells (Fig. 148). The crystalline cone, in contradistinction to its variability in the eyes of Insects, is never lacking and is often composite and divided into three segments, a

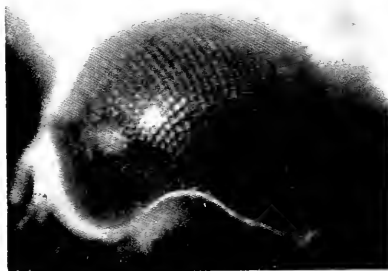


FIG. 146.—THE EYE OF A CRAYFISH.

Showing the faceted appearance of the compound eye (Norman Ashton).

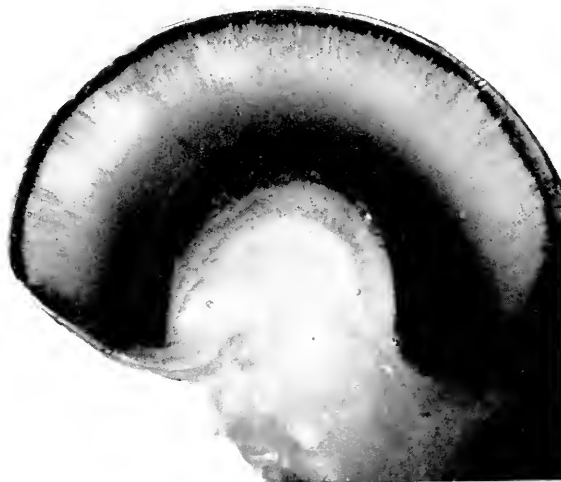


FIG. 147.—HEMISECTION OF THE EYE OF THE LOBSTER (see Fig. 693) (Norman Ashton).

¹ See Grenacher (1879), Chun (1896), Rosenstadt (1896), Parker (1897), Nowikoff (1900), Wenke (1908), Hesse (1908), Strauss (1909), Demoll (1909-17), Doflein (1914), Bernards (1916), Herter (1928), Fricke (1931), Hanström (1931-35), Welsh (1937), Heberer and Kupka (1942).

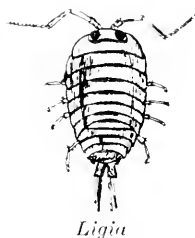
short outer, a main intermediate, and a hollow inner segment. The retinule consists of relatively few cells (4 in crabs) grouped around the central rhabdome, the proximal extremity of which rests on a fenestrated membrane. There is evidence that the retinular cells are not all of the same kind; thus 3 different types have been described in the Isopod, *Ligia* (Ruck and Jahn, 1954). In some species (the crayfish, *Astacus*, and the shrimp, *Crago*) the nuclei of the retinular cells are arranged in three zones, a configuration somewhat reminiscent of the multi-layered retina of Vertebrates; it is to be remembered, however, that all are derived from the hypodermal cells of the integument.

The pigmentation is complicated, for each ommatidium possesses at least two functionally different pigments. Pigmentary cells (IRIS CELLS) containing melanin surround the distal part of each ommatidium: the proximal part is similarly ensheathed or the retinular cells themselves also contain melanin; while at the level of the retinule is a clear reflecting pigment¹ contained in separate cells; this by reflection prevents the entry of oblique rays. Although the pigmentary cells do not move, the melanin pigment within them shows marked migratory changes (Welsh, 1930-41; Parker, 1932; Bennitt, 1932) (Fig. 148). In bright light the black pigment in the iris cells meets that in the retinular cells so that the entire ommatidium is encased in a sleeve of pigment: in dim light the pigment in the iris cells migrates distally to lie between the cones, that in the retinular cells migrates to a position proximal to the basement membrane, while the reflecting particles surrounding the retinal elements, cleared of absorbing pigment, act as a functional *tapetum*. We have already seen that the migration of these pigments often shows an autochthonous diurnal rhythm² and that, in addition to this response to the direct action of light, they are under a complex hormonal and nervous control (Kleinholz, 1936-38; Welsh, 1939-41; Brown, 1944; and others).³

¹ The chemical nature of the reflecting pigment varies. In the crayfish, *Astacus*, the iris tapetum is of uric acid, in the lobster, *Homarus*, uric acid is supplemented by at least 3 other substances, none of which is guanine (Kleinholz and Henwood, 1953; Kleinholz, 1955).

² p. 19.

³ See further p. 554.



Ligia

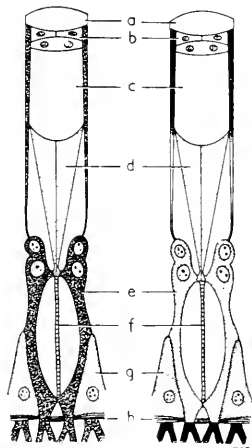
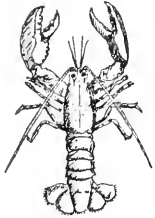


FIG. 148.—THE OMMATIDIUM OF THE CRAYFISH, *ASTACUS*.

On the left, in the light-adapted, and on the right, the dark-adapted state.

a, Cornea; b, hypodermal corneal cells; c, body of crystalline cone; d, inner segment of crystalline cone; e, retinal pigment cells; f, rhabdome separating retinular cells; g, tapetal cells; h, basement membrane (modified from Bernhards).



Lobster



Prawn

We shall see¹ that the stalked eyes of such Decapods as the lobster, the shrimp and the prawn are remarkable in that the nervous connections run to the procephalic lobes of the cerebral ganglion up the long stalks containing the optic lobe with its series of ganglia and intervening plexiform zones. The presence of a three-layered compound retina and a ganglionated optic lobe makes these crustacean eyes the most complex among Invertebrates (Figs. 147, 693).

The eyes of Crustaceans living at ocean depths are rarely so well formed as those inhabiting littoral or shallow waters; as a rule—to which, however, there are marked exceptions, particularly in the more active forms—the number of ommatidia in bathypelagic forms is decreased and the pigment is scanty or absent so that the organ functions as a superposition eye² adapted for dim illumination (Edwards and Bouvier, 1892).

THE COMPOUND EYES OF INSECTS

The compound eye of Insects has excited interest and admiration for centuries (Figs. 149 and 150)³; indeed, the faceted cornea attracted the attention of the pioneer Dutch microscopist, van Leeuwenhoek,

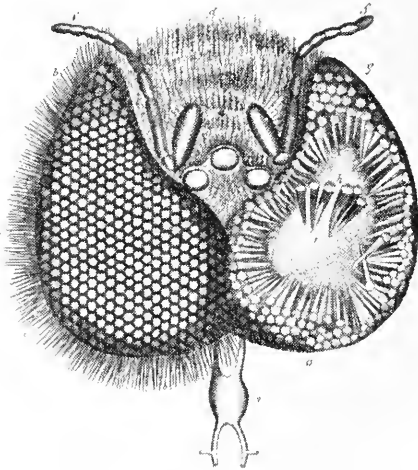


FIG. 149.—THE EYES OF INSECTS.

An old anatomical drawing from Swammerdam (*Bybel der Nature*, Leyden, 1737).

Although inaccurate in details, the surface of the intact compound eye is seen on the left, a partially dissected eye on the right, as well as the 3 central ocelli (reproduced by permission of the Cambridge University Library; by courtesy of Dr. Pirenne and the Pilot Press).

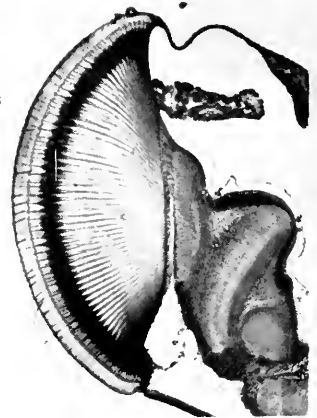


FIG. 150.—THE COMPOUND EYE OF THE BEE.

Section through the compound eye, showing the optic lobe consisting of 3 optic ganglia, and the protocerebrum (below) (Norman Ashton).

¹ p. 521.

² p. 169.

³ For the descriptive anatomy of the compound eyes of insects, see Müller (1826), Grenacher (1879), Exner (1891), Hesse (1901–8), Seaton (1903), Dietrich (1909), Johnas (1910), Bedau (1911), Geyer (1912), Demoll (1912–17), Zimmermann (1913), Jörschke (1914), Magnion and Popoff (1914), Priesner (1916), Ast (1920), Cajal and Sánchez

at the end of the seventeenth century. Each individual ommatidium has a relatively simple structure similar to that already described in Crustaceans. Most externally is the focusing apparatus, made up from without inwards of a cuticular lens-like formation (the corneal lens or facet) under which lies the crystalline cone surrounded by nucleated hypodermal cells which do not form a complete layer as in the typical crustacean eye (Fig. 151).

Such a dioptric apparatus forms the typical arrangement (the EUCCONE EYE); but variations occur in which the entire refractive



Colorado beetle
(Coleoptera)

FIGS. 151 AND 152.—SCHEMATIC STRUCTURE OF THE TWO TYPES OF OMMATIDIA OF INSECTS.

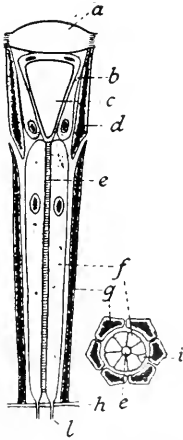


FIG. 151.—The apposition eye, with (alongside and below) a section through the retinule.

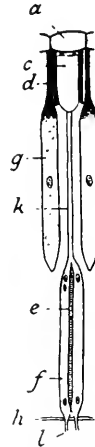


FIG. 152.—The superposition eye in the dark-adapted condition with the pigment in the iris cells almost entirely withdrawn into their upper extremities.

a, corneal facet; *b*, corneal cells; *c*, crystalline cone; *d*, iris pigment cells; *e*, rhabdome; *f*, sensory cells of the retinule; *g*, retinal pigment cells; *h*, fenestrated basement membrane; *i*, eccentric retinal cell; *k*, filament connecting crystalline cone with rhabdome; *l*, nerve fibre (after Weber and Snodgrass).

function is taken over by the cornea. In place of a separate crystalline cone secreted by special crystalline cells (*vitrella*), these cells may merely secrete an accumulation of fluid (the PSEUDOCONE EYE), as occurs in Muscids. In other types, such as beetles (Coleoptera), some bugs (Hemiptera) and crane-flies (Tipulids), the cones remain cellular and non-refrigent (the ACONE EYE). Alternatively, the refractive



Crane-fly
(Tipulidæ)

(1921), Corneli (1924), Kuhn (1926), Götze (1927), Bott (1928), Friederichs (1931), Nowikoff (1931), Werringloer (1932), Weber (1934), Lüdtke (1935-51), Wundrig (1936), Vidal and Courtis (1937), Zänkert (1939), Verrier (1940), Lhoste (1941), Roonwal (1947), Ehnborn (1948), Tuurala (1954), Fernández-Moran (1956).

*Dytiscus*

functions of the crystalline structure may be replaced by the cuticular cornea which itself forms a cone-like invagination, as occurs in fire-flies (Lampyrids) or the water-beetle, *Dytiscus* (the EXOCONE EYE), an arrangement reminiscent of that seen in the king-crab (Fig. 143).

In most diurnal insects the retinule with its tubular arrangement of a group (usually 7 or 8) of elongated sensory cells arranged around the central rhabdome lies immediately underneath the lens, resting upon a fenestrated basement membrane through which pass nerve fibres which run to the outermost nucleus of the optic lobe.¹ Around the bases of the retinular cells in close association with the basement membrane are refractile TRACHEÆ which increase the optical efficiency

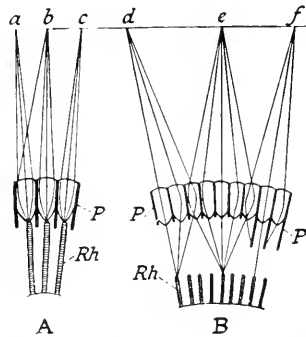


FIG. 153.—IMAGE FORMATION IN THE COMPOUND EYE.

A, apposition eye. Only the rays of light falling normally (or practically so) (*a*, *b*, *c*) reach the rhabdomes and retinular cells so that each ommatidium functions as a unit. The ray from *b* deviating to the left is absorbed by the pigment sheath, *P*. (Compare Fig. 156.)

B, superposition eye. The main part of the diagram shows the pigment in the dark-adapted position drawn up between the cones in which case the superposition optical system is effective; thus the rays from *d* and *e* can traverse many ommatidia to become focused on one rhabdome, *Rh*. In the two ommatidia on the right the pigment is in the light-adapted position so that all rays except those entering normally (or nearly so) on the facet are intercepted by the pigment, *P*.

of the eye by reflecting the light back through the rhabdome, thus serving the function of a *tapetum*. As in Crustaceans, pigment is usually a prominent feature. In most diurnal insects each ommatidium is entirely ensheathed by pigmented cells arranged in two sections, the *iris pigment cells* or *primary iris cells* lying distally surrounding the crystalline cones, and the *retinal pigment cells* or *secondary iris cells* lying proximally which encircle the retinule; the ommatidium thus functions as an isolated unit. The iris cells contain not only light-absorbing pigment but also pale or coloured reflecting granules which serve a tapetal function.

¹ p. 521.

While this is the most common form of compound eye wherein each ommatidium is designed to act by itself with the result that the optical image resembles a finely grained mosaic (the *apposition eye*),¹ many nocturnal insects show a dramatic contrast wherein light is utilized more effectively by an arrangement which allows incident rays from several facets to reach one rhabdome (the *superposition eye*). The typical structure of this type of eye is seen in beetles and noctuid moths (Fig. 152). In these the retinule is situated far back and the interval between it and the crystalline cone is traversed by a non-refractile translucent filament connecting this structure with the rhabdome, while the pigmented iris cells are concentrated distally between the crystalline cones leaving the retinules without an insulating sheath.

FIGS. 154 AND 155.—SUPERPOSITION IMAGES FORMED BY THE REFRACTIVE SYSTEM OF *LAMPYRIS*.



FIG. 154.—The mosaic of images formed at a level immediately beneath the optical system.



FIG. 155.—The superimposed images at the level of the rhabdome (after Exner).

The functional contrast between the two types is seen in Fig. 153. In Figs. 154 and 155 are seen the illustrations from Exner's (1891) classical treatise showing the image of a candle flame formed by the corneal facets and cones of the fire-fly, *Lampyrus*. When the microscope is focused just below the dioptric apparatus a multitude of luminous spots is seen all of which become merged into one at the level of the rhabdomes. The light from as many as 30 different facets may thus be concentrated on one of these structures.

Intermediate forms between these two types of compound eye exist; nor are they mutually exclusive. Thus in Mantids the two are seen combined in the same eye; the anterior ommatidia which are used for binocular vision are of the apposition type while the lateral parts are of the superposition type (Friza, 1928)—a functionally efficient arrangement. Moreover, as in Crustaceans, the change from a superposition eye of the nocturnal type to an apposition eye of the diurnal type with its high degree of resolution can be made functionally



Fire-fly

¹ p. 173.



Butterfly
(*Vanessa*)

by a migration of pigment, thus effecting an adaptive process in species which are active both by day and by night : in dim light the pigment becomes concentrated anteriorly so that the eye can function as a superposition eye and make full use of all the available light ; while in bright illumination it disperses and migrates posteriorly surrounding each retinule with an opaque mantle intercepting all lateral rays (Parker, 1932). Thus in the dark-adapted state examination of the eyes of certain noctuid moths with an ophthalmoscopic mirror shows a luminous red reflection from a group of ommatidia ; in the light-adapted state there is a minute glow from one central ommatidium only (Demoll, 1917 ; Horstmann, 1935). This pigmentary migration in some butterflies and moths begins from half to one hour before sunrise or sunset and the change occupies an interval varying from a few minutes to an hour (Merker, 1929-34 ; Collins, 1934). The excised eye always adopts the light-adapted distribution of pigment. The migratory response is abolished by narcosis nor does it occur in butterflies when the insect is at rest and inactive (Demoll, 1909-11 ; Day, 1941). Its mechanism is unknown ; a purely hormonal control is improbable since individual ommatidia may respond to localized illumination (Day, 1941) ; but whether the migration of pigment is dependent upon nervous reflexes from the retinule or is initiated by photochemical reactions within the pigmentary cells is controversial.



Notonecta

Pigmentary migration of a less dramatic kind occurs in certain purely apposition eyes of diurnal species as a response to rapid changes in illumination. These are associated chiefly with the pigment in the cells around the basement membrane (butterflies—Demoll, 1909 ; the water-boatman, *Notonecta*—Bedau, 1911). In the latter the visual cells also elongate in the dark-adapted state (Lüdtke, 1951-53).

The Optical System of the Compound Eye

The optical system of the compound eye has always excited considerable interest since it was first studied by Johannes Müller (1826) ; Fig. 156, taken from his classical work on this subject, indicates characteristically his conception of the optical mechanism whereby a point source of light excites only one (or two) ommatidium. In his *Mosaic Theory* he showed that an image of considerable definition would be formed by the juxtaposition of the many small luminous stimuli received by the ommatidia, each of them the impression of the corresponding projection in the visual field, each of them varying according to the pattern of the incident light. Such an image, in comparison with that formed by the eye of Vertebrates, is erect, and the effect can be easily simulated by allowing light to traverse a bundle of narrow tubes and fall upon a plate of ground-glass, an arrangement

which clearly shows that the definition of the image depends on the number of tubes per unit area (Alverdes, 1924). Using the excised anterior segment of the eye of the fire-fly, *Lampyrus*, as a lens, Exner (1891) succeeded in photographing the image (Fig. 157); the degree of resolution thus obtained has been estimated by Marchal (1910) to

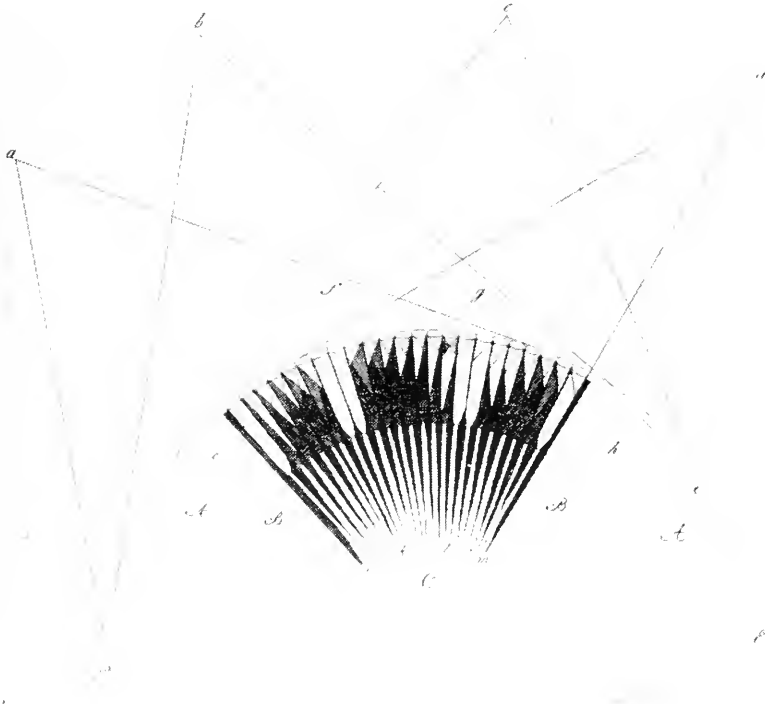


FIG. 156.—THE COMPOUND EYE ACCORDING TO JOHANNES MÜLLER.

When light emitted by different points, *a*, *b*, *c*, *d*, falls on the eye, that from *a* completely illuminates cone *e*, but the ommatidia to the right of *e* are not illuminated all the way down. Only the nerve *i*, issuing from cone *e*, is thus stimulated by the source *a*, while light from the same source entering other ommatidia is unable to stimulate the fibres since it is absorbed by the pigment sheaths. Similarly, light from *b*, stimulates two ommatidia at *f*; light from *c*, two ommatidia at *g*; and light from *d*, one ommatidium at *h* (from Müller, 1826; by permission of the Cambridge University Library; by courtesy of Dr. Pirenne and the Pilot Press).

correspond approximately to an acuity of $1/60$ in the human eye. It is important to realize that owing to the isolating effect of the pigment mantle, no formed image is produced at the level of the receptor cells; each of these acts only as a photometer and from the mosaic thus formed by the individual ommatidia the picture of the outside world is synthesized in the central nervous system (van der Horst, 1933).

*Musca*

Dragonfly

*Necrophorus**Apis*

In the compound eye of the winged male of *Lampyris* there are 2,500 ommatidia ; but the number of elements varies considerably between different species depending largely on their habits. Thus, in *Solenopsis*, the worker-ants which live underground have 6 or 9, while the winged males which pursue the female in the air are provided with 400 ; in genera with a high visual acuity the numbers are much higher—in the house-fly, *Musca*, 4,000 ; in the water-beetle, *Dytiscus*, 9,000 ; and in dragonflies (Odonata) up to 28,000 (Demoll, 1917 ; Imms, 1935), or the burying beetle, *Necrophorus*, 29,300 (Leinemann, 1904). The size of the individual facets remains fairly constant (15 to 40 μ) ; the size of the eye is determined essentially by their number.

From the functional point of view, however, the most important feature is the OMMATIDIAL ANGLE, that is, the angular extent of the visual field covered by each element. It is obvious that if a pattern is to be resolved, two adjacent ommatidia must be unequally stimulated so that their angular separation must form the anatomical basis of the visual acuity, corresponding in man to the inter-cone distance and determining the fineness of the "grain" of the resulting picture (del Portillo, 1936). As this angle becomes smaller, the resolving power increases, but less light will enter each facet. Thus the angle in the bee, *Apis*, varies from 0.9° to 1° in the centre of the eye, and in the earwig, *Forficula*, is 8°, so that the latter will obtain a single point of light as the image of an object which the eye of the bee will resolve into 64 (Baumgärtner, 1928 ; v. Buddenbrock, 1937). In the locust, *Locusta*, the ommatidial angle is about 21° (Burt and Catton, 1954). In the periphery of the eye the ommatidial angle is larger than in the centre and the acuity correspondingly less ; in the anterior region of the eye it is often smaller than in the central, an arrangement which favours visual acuity in flight (Auer, 1949) (Fig. 158).

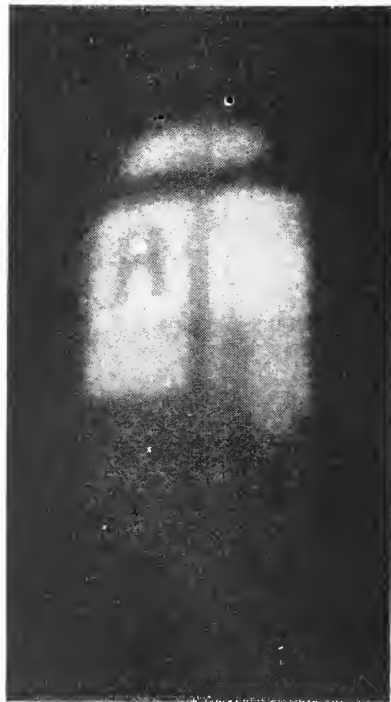
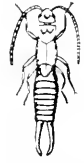


FIG. 157.—EXNER'S CLASSICAL PHOTOGRAPH THROUGH THE OPTICAL SYSTEM OF THE COMPOUND EYE OF *LAMPYRIS SPLENDIDULA*.

Showing a window with a letter R on one pane and a church beyond (from Wigglesworth's *Principles of Insect Physiology*, Methuen).

Exner's early work on the dioptries of the ommatidial system still remains classical. He showed that the essential refractive device is the crystalline cone, which, of course, unlike the lens of Cephalopods and Vertebrates, has a fixed focus incapable of adjustment. The crystalline cone itself is composed of concentric lamellae the refractive index of which increases progressively from the periphery to the central axis (Fig. 159) ; it therefore acts as a " lens-cylinder " wherein an obliquely incident ray is progressively refracted until it is gradually



Forficula

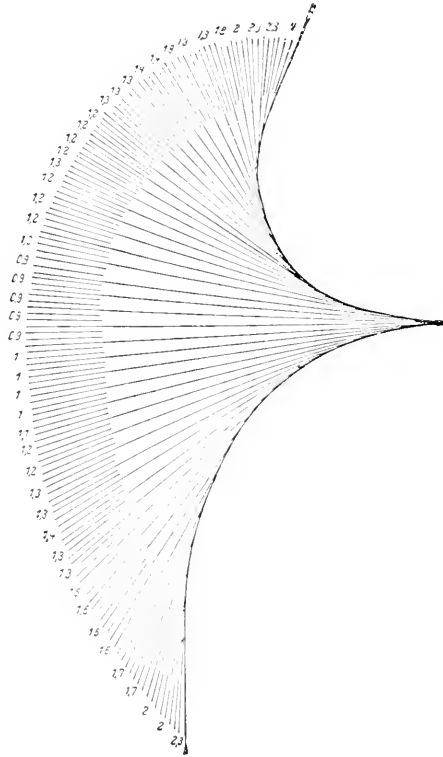


FIG. 158. - THE OMMATIDIAL ANGLES OF THE EYE OF THE HONEY-BEE.

The ommatidia are drawn in groups of 3, and the drawing shows the way in which an ommatidial angle varies in different parts of the eye ; the values of the angles are given in degrees (Pirenne, after Baumgärtner).

brought back to the axis. It is probable that the crystalline cone thus brings the image formed by an ommatidium to a small point although different wave-lengths will be brought to a focus at different places (Goulliart, 1953). To some extent therefore, the optics of the compound eye with its many elements is comparable to the analysis made by television.

The appositional eye wherein the retinule abuts against the crystalline cone may be compared optically to such a system wherein rays of light pass through a lens-cylinder of a length equal to its focal distance (Fig. 160). In this event a beam of parallel light (*mpn*) entering perpendicularly to one edge of the cylinder (*ab*) will be focused as an inverted image at *y* on the other edge and will



Locusta

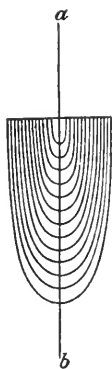


FIG. 159.—THE LENS CONE OF THE COMPOUND EYE.

The laminated optical structure of superimposed lamellæ (after Exner).

emerge as a diverging beam ($m'p'n'$). Oblique rays (q) will emerge at an angle as q' . The pigment mantle around the cones, however, will absorb oblique rays and virtually permit the light to emerge only at y , where the image falls as a single luminous point on the subjacent retinule; the apposition of all such points will form the complete erect image perceived by the eye.

In the superpositional eye, on the other hand, the optical system will correspond to a lens-cylinder of a length equal to twice its focal distance (Fig. 161). The inverted image of a distant object will be formed in the middle of the cylinder (xy); the rays traversing the remaining half of the cylinder will pursue a symmetrical course and emerge at an angle (β) equal to that at which they entered (α) but opposite in direction. Not only will normal rays thus fall on the distant rhabdome but also oblique rays refracted from the cones towards the same side from which they have come, so that a number of separate images can be superimposed on one visual element. The resultant image thus gains in luminosity at the sacrifice of resolution.

The ability to analyse the plane of polarized light is a common function of the compound eyes of Arthropods and of both the simple and compound eyes of Insects; it is a function which is freely used to aid orientation out-of-doors.¹ The structure which serves as an analyser, however, has given rise to controversy. The suggestion that

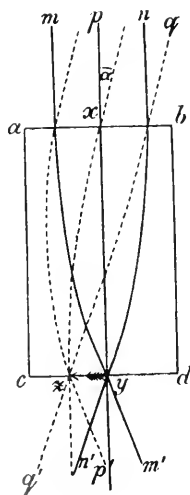


FIG. 160.—THE OPTICAL SYSTEM OF THE APPPOSITION EYE.

The lens cylinder is equal in length to its focal distance (after Exner).

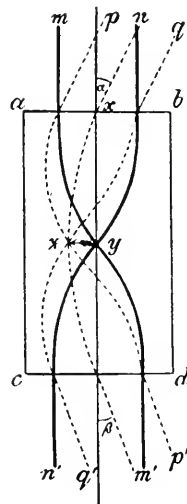


FIG. 161.—THE OPTICAL SYSTEM OF THE SUPERPOSITION EYE.

The lens cylinder is equal in length to twice its focal distance (after Exner).

¹ p. 66. See Kalmus. *Nature* (Lond.), **184**, 228 (1959).

the reticular cells act as differentially orientated detectors¹ was based on differences in the electrical response with variations of the direction of polarization of the incident light. Such a suggestion, however, is difficult to accept if it is agreed that the individual cells are not furnished with corresponding axonal transmission²; the theory could not be made to adapt itself to the proven single impulse transmitted from each entire ommatidium in the eye of *Limulus* (Waterman, 1950; Waterman and Wiersma, 1954); moreover, such a change does not seem to be invariable.³ It has also been suggested that the ultra-structure of the rhabdome with its composite laminated and fenestrated bodies, could provide a physical basis for this faculty (Fernández-Moran, 1956). An alternative hypothesis is that the responsible structure is the corneal facet with its chitinous covering which is birefringent, rather than any structure within the ommatidium (Waterman, 1951; Berger and Ségal, 1952). Wolsky (1929) and Stockhammer (1956), however, were unable to detect any optical mechanism which could act as an analyser in the entire dioptric apparatus in the insects which they studied, and concluded that this mechanism resided in the visual cells. It is obvious that further research is required on this problem, and it may well be that more than one mechanism is operative, differing in different species, or a mechanism as yet unsuspected.

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¹ Autrum and Stumpf (1950), Menzer and Stockhammer (1951) in the bee; Stockhammer (1956) in Diptera and Hymenoptera.

² p. 158.

³ de Vries *et al.* (1953), in the blowfly, *Calliphora*.

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CHAPTER VII

THE SYSTEMATIC ANATOMY OF INVERTEBRATE EYES

FROM the morphological point of view we have seen that the visual organs of Invertebrates show an astonishing range in structure, varying in complexity from the simple eye-spot or the single visual cell to the elaborate organs characteristic of Cephalopods or Insects ; from the functional point of view the variation is equally great, evolving from a primitive and perhaps undifferentiated sentience which may influence metabolic and motorial reactions, to the capacity to form elaborate images whereby intensity, hue, form and spatial relationships can be differentiated with sufficient exactitude and appreciation to determine behaviour. The curious thing, however, is that in their distribution the eyes of Invertebrates form no series of contiguity and succession. Without obvious phylogenetic sequence, their occurrence seems haphazard ; analogous photoreceptors appear in unrelated species, an elaborate organ in a primitive species¹ or an elementary structure high in the evolutionary scale,² and the same animal may be provided with two different mechanisms with different spectral sensitivities subserving different types of behaviour.

A striking example of this is seen in the flat-worm, *Planaria lugubris*, which has both positive and negative photo-reactions (Viaud and Médioni, 1949) ; if this animal is bisected the photo-positive reactions appear in the posterior segment before the nerves regenerate suggesting that these responses are due to dermal sensitivity, while it has been shown that the photo-negative reactions are due to the eyes ; photokinesis is dependent on the skin, positional orientation to light on the eyes. In the earthworm, *Lumbricus terrestris*, on the other hand, the photo-negative reactions in bright light are controlled by the head-ganglion, while the photo-positive reactions in dim light are mediated by the ventral cord ; the two activities are mutually antagonistic but normally the cephalic mechanism is dominant (Prosser, 1934). Again, the possession of both ocelli and compound eyes by many insects, the first sometimes reacting to polarized light and orientative in function, and the second to ordinary light as well and also subserving form vision, is an example of two mechanisms which are supplementary in function and not antagonistic (Wellington, 1953).

We shall now discuss the occurrence of these organs in the invertebrate phyla, referring back to the previous chapter for a description of their minute structure.

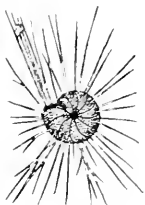
¹ Such as the complex eye of the jelly-fish, *Charybdea* (p. 183).

² Such as the simple eyes of Insects (p. 224).

TYPICAL PROTOZOA

[Drawn not to scale, but approximately to a standard size.]

SARCODINA

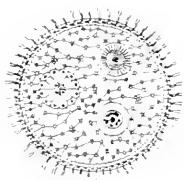
*Amoeba*

Foraminifer

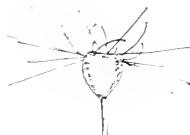


Radiolarian shell

FLAGELLATA

*Euglena**Volvox**Trypanosoma**Trichomonas**Noctiluca*
(see Fig. 886)*Gonyaulax*
(Dinoflagellate)

CILIOPHORA

*Paramecium**Vorticella**Stentor*

Sueterian

SPOROZOA

Sporozoite
of
Plasmodium

Protozoa

PROTOZOA are the most primitive and simplest of animals, some of which might with equal justification be considered as plants ; they are essentially single-celled but sometimes form loose colonies by budding or by cell-division, showing some degree of co-ordination but never forming differentiated tissues. Of all animal types they are the most numerous, being found in every continent, on land, in fresh water, in the seas and impartially distributed as parasites within all animals (including some of their own kind), among which not the least frequented is Man ; their skeletons contribute largely to the oozes of the seas and to the composition of the rocks of which the land-masses are made.

Within the phylum four methods of activity are evident—amœboid movement, flagellate and ciliary progression, and encystment with spore-formation, characteristics under which the upwards of 15,000 species may be conveniently grouped into 4 classes (see p. 179).

SARCODINA (or RHIZOPODA), organisms which progress by sending out finger-like pseudopodia into which the protoplasm of the cell pours itself. This class comprises such types as the fresh-water *Amœba*, the parasitic *Entamœba* or the marine Foraminifera with chalky shells and Radiolaria with siliceous shells which after death enter largely into the formation of the oozes of the bed of the ocean.

FLAGELLATA (or MASTIGOPHORA), organisms which swim by the lashing movements of one or a few whip-like flagella. The class comprises such types as the common *Euglena* and colonial forms such as *Volvox* almost universal in fresh-water ponds, the parasitic, disease-producing Trypanosomes and Trichomonads, Dinoflagellates including *Noctiluca* which gives luminescence to the seas,¹ and Cystoflagellates, important constituents of the plankton of lakes and the oceans.

CILIOPHORA, organisms which progress by the coordinated movements of many hair-like cilia. The class comprises the Ciliates (such common types as the slipper-shaped *Paramecium*, the bell-shaped *Vorticella* or the trumpet-shaped *Stentor*) and the Suctorians which lose their cilia in adult life and in their place develop tentacles used as suckers by which they capture and suck out the bodies of their protozoan prey.

SPOROZOA, encysted organisms without a locomotive mechanism ; they are parasitic on almost every species of animal and are spore-forming in habit (Coccidia, Haemosporidia, *Plasmodium*, etc.).

In view of the fact that the response to light in these primitive forms is motorial, it is not surprising that receptors are not found in the passive parasitic Sporozoa ; in the first three classes responses to light are found among the freely-swimming active types, but as would be expected in unicellular organisms, the receptor mechanisms are of the most primitive nature. In the Sarcodina (*Amœba*) and some Ciliates

¹ p. 738.

(*Paramœcium*) sensitivity to light is diffuse ; in other Ciliates (*Stentor*) it is localized to a part of the organism but without apparent specific mechanism ; but even at this primitive unicellular stage an obvious localization of function may be attained by the development of an EYE-SPOT and the efficiency of the organelle increased, particularly in the acquirement of a crude directional appreciation, by the provision of pigment (as in *Euglena*)¹ or even of a primitive refractile mechanism (as in some Dinoflagellates).²

Parazoa

The SPONGES (PORIFERA), sessile marine animals which form living thickets in the sea, represent a cul-de-sac in evolution between Protozoa and Metazoa dating back almost to the beginning of geological records. They are the simplest multicellular animals and show the beginnings of the development of a "body" composed of tissues ; but although there is cellular differentiation there is little cellular co-ordination. Being vegetative and sedentary in habit they have no need of sense-organs as they lie moored to rocks or sea-weed. They possess no nerve cells but the body cells retain properties of an irritability of a low level ; and in the active larval forms of certain types (the simple sponge, *Leucosolenia*) apolar light-sensitive cells of the most elementary type have been described (Minchin, 1896).



Leucosolenia



Sycon

Invertebrate Metazoa

In Metazoa—which includes all animal species apart from the Protozoa and Parazoa—the development of specialized cells and their eventual co-ordination into distinct organs allow the evolution of specific sensory activities as the term is generally understood. These we shall now study, but it must be remembered that the Invertebrates (or Non-chordates) do not form a homogeneous sub-kingdom but rather represent an assemblage of unrelated groups of animals which have little in common except the negative attribute of not being provided with a dorsal nerve-cord with its supporting axis or with gill-slits. From our restricted point of view there is the dramatic difference that (with few exceptions) the eye when present is developed from the skin, while in Vertebrates it originates as an outgrowth of the brain.

CŒLEENTERATA

CŒLEENTERATES are simply formed animals with a body-cavity (cœlom) and digestive cavity (enteron) combined so that the body is formed as a sac with an opening at one end only. They show the beginnings of separate organs with a consequent division of labour, and among them

¹ p. 126.

² p. 126.

*Hydra**Obelia* medusoid*Obelia* polyp

Sea-anemone

Comb jelly
(see Figs. 887-8)

visual structures of some complexity first make their appearance. The phylum may be divided into two sub-phyla—the CNIDARIA, provided with numerous stinging cells (*κνίδη*, a nettle), and ACNIDARIA, wherein these are replaced by adhesive cells. The first-sub-phylum is divided into 3 classes :

HYDROZOA, comprising solitary polyps such as the fresh-water *Hydra*, the marine Hydroids, branching colonial polyps of vegetative appearance liberating freely-swimming Hydromedusæ (*Obelia*, *Sarsia*, etc.) and some pelagic colonial forms.

SCYPHOZOA ("cup animals"), marine jellyfish, free-swimming medusæ, typically umbrella-shaped with the important organs situated on the margin or under-surface.

ANTHOZOA ("flower animals"), sessile marine polyps with no medusa-forms, such as sea-anemones, sea-fans, sea-pens and corals.

ACNIDARIA, comprising the Ctenophora (comb-jellies or sea-gooseberries), delicate freely-swimming globular organisms, pelagic in habit, gelatinous and transparent, beautifully iridescent in the sunlight and often luminescent in the dark,¹ provided with comb-like rows of cilia.

The degree of elaboration of the visual receptors varies with the motility of the organism, and many Cœlenterates are sessile, plant-like zoophytes ; eyes are therefore confined to the mobile medusæ and these are of a very primitive nature,² while the sessile polyps of this phylum (hydroid forms and all Anthozoa) have no sense organs or, at most, contact photoreceptors of the most elementary type.³

The Ctenophora are provided with a sense organ at the upper pole of the organism consisting of a mass of limestone particles supported on cilia associated with sensory cells communicating by nerve fibrils with the swimming-combs; this is considered to act as a statocyst or balancing device and visual organs are absent.

Among the Hydrozoa, some fresh-water forms are sensitive to light but possess no detectable visual organs : a hydra, for example, will migrate towards the lighted side of its container where, incidentally, there are usually more food-organisms. In some freely-swimming Hydromedusæ, however, externally visible light-sensitive organs provided with sensory cells and pigment and sometimes a refringent apparatus may be found in the tentacular bulbs at the bases of the tentacles (Fig. 162) ; these take the form of

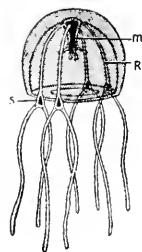


FIG. 162.— THE MEDUSOID FORM OF *BOUGAINVILLEA* (*MARGELIS*). M, manubrium; R, radial canal; S, sense organ (after Allman).

¹ 739.
² For detailed information, see O. and R. Hertwig (1877), Schewiakoff (1889), Ber. 1898), Linko (1900), v. Uexküll (1909), Lehmann (1923).
³ 16.

a primitive flat eye, as in *Turris* or *Lizzia* (Fig. 96), or are invaginated as an elementary cupulate eye, as in *Sarsia* (O. and R. Hertwig, 1878 ; Jourdan, 1889). These organisms are light-sensitive and extirpation of the tentacular bulbs with the ocelli completely abolishes the response to light.

Among the jellyfish (Scyphozoa) more elaborate organs are seen. In the common jellyfish, *Aurelia aurita*, which is found in great shoals around the British coast, eight sense-organs (TENTACULOCYSTS) arise as modifications of tentacles ; each, lying in the protection of a marginal

FIGS. 163 AND 164.—THE COMMON JELLYFISH, *AURELIA AURITA*.

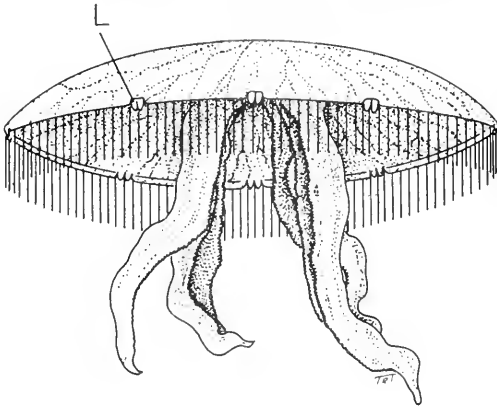


FIG. 163.—Side view of the jellyfish, showing the numerous marginal tentacles hanging from the border of the convex umbrella, and the dependent oral arms. The margin of the umbrella is broken by 8 notches, the marginal lappets (L).

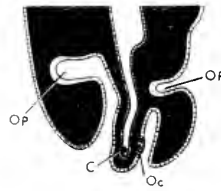


FIG. 164.—A marginal notch, showing a tentaculocyst comprised of two olfactory pits, OP, a calcareous concretion, C, and an ocellus, OC (modified from Lankester).

niche, has three types of sensory cells—red or black pigmented cells responding to light, “olfactory” cells with a chemical appreciation, and club-like cells containing calcareous concretions with a balancing function (Figs. 163–4).

Exceptionally, as in the Cubomedusan, *Charybdea*, a large ocellus has been reported with a cellular lens, a vitreous structure and a complex retina—an organ structurally capable of some degree of visual imagery (Fig. 102) (Schewiakoff, 1889 ; Berger, 1898). The biological value of this elaboration in a brainless organism is somewhat speculative.

ECHINODERMATA

Among ECHINODERMS (“spiny skinned”), a phylum characterized by its radial symmetry, visual organs are rudimentary. This would



Starfish



Brittle-star

be anticipated from the absence of centralization in the nervous system, associated presumably with the absence of a head region, and from the characteristically sluggish and sedentary habits of its members. The phylum is divided into 5 extant classes :

ASTEROIDEA, or starfishes, motile but sluggish organisms.

OPHIUROIDEA or brittle-stars, resembling starfishes but with the arms sharply marked off from the central disc.

ECHINOIDEA or sea-urchins, living off rocky coasts, with a round pin-cushion-like body covered with plates and provided with long sharp spines.

HOLOTHUROIDEA or sea-cucumbers, worm-like creatures with calcareous plates, occurring in most seas.

CRINOIDEA, sea-lilies or feather-stars, stalked forms anchored on rocks or

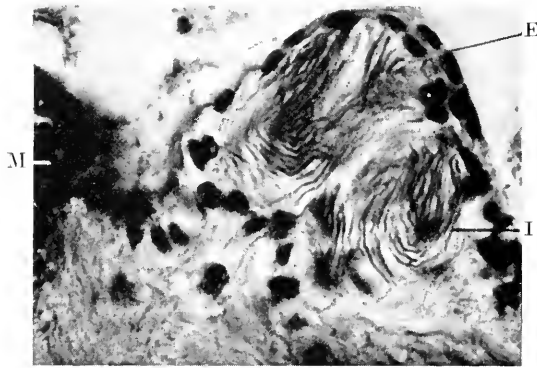


FIG. 165.—THE IRIDOPHORES IN THE SEA-URCHIN, *DIADEMA ANTILLARUM*.

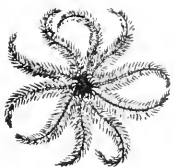
Section through a cluster of iridophores, I; E, epidermal layer; M, melanophores, underneath which lies the superficial nerve layer (fixed Bouin; stained Masson's argentaffine reaction; counter-stained Mallory's triple stain. (Approx. $\times 500$) (N. Millott).



Sea-lily

in mud usually at great depths, with appendages (cirri) and branching arms growing from a central cup; feather-stars become free-swimming in adult life.

In most Echinoderms the skin is diffusely sensitive to light, particularly in sea-cucumbers (Crozier, 1914-15); in brittle-stars and feather-stars there are no special sense organs; in sea-cucumbers sense organs are represented by statocysts sometimes present at the bases of the tentacles, and tactile processes sometimes present on the dorsal surface of some of the creeping forms; "eyes" are present only in starfishes.



Free-swimming
feather-star

The diffuse dermatoptic sense shows interesting variations. Thus in some starfishes the body-surface is said to be sensitive to changes in intensity, the poles and skin gills to steady light; in some sea-cucumbers (*Synapta*) the whole surface is sensitive to both, while in others (*Holothuria surinamensis*) the rim of the body is particularly sensitive, the posterior end and tentacles less so and the head least. In the sea-urchin, *Paracentrotus lividus*, the apical poles are

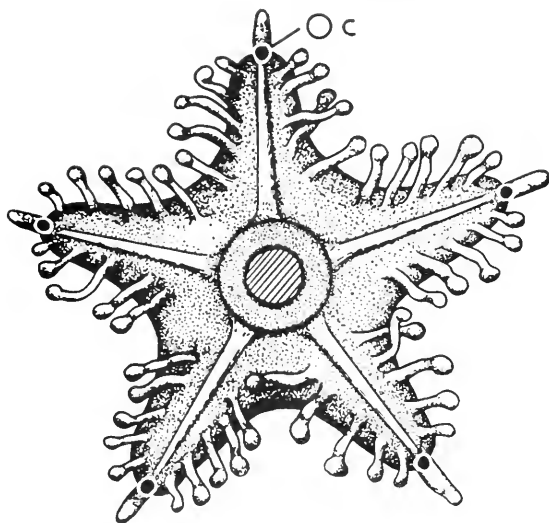


FIG. 166.—DIAGRAM OF A VERY YOUNG ASTEROID

At the base of the 5 terminal tentacles is an optic cushion with a bright red ocellus, Oc, connected by an epidermal radial nerve which runs to the central nerve pentagon surrounding the mouth (after Lang). Compare Plate I.

said to show the most rapid reactions (Scheer, 1956). In the Echinoid, *Diadema*, the distribution of sensitivity corresponds to the distribution of the nerve elements and it may be that these are directly stimulated by light as we have seen to occur in the apolar light-sensitive cells of worms (Millott, 1954). On the other hand, photosensitive pigments may be present in minute quantities, but there is yet no evidence as to their nature.

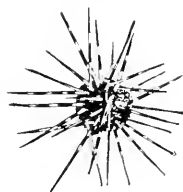
Many SEA-URCHINS have the same primitive sensitivity associated particularly with their pigmented spicules which move on the stimulus of light (v. Uexküll, 1900), and in some types characteristic iridescent bodies associated with melanin pigment lie near the spines (*Diadema antillarum*) (P. and F. Sarasin, 1887; Dahlgren, 1916; Millott, 1950-54). These represent clusters of regularly arranged plates resembling iridophores¹ in their arrangement, which presumably act by reflecting the light onto the sensitive spines (Millott, 1953) (Fig. 165). It is of historical interest that the Sarasins (1887), in a much quoted paper, described similar structures in *Diadema setosum*, an allied species inhabiting the Indian Ocean, as being "eyes" composed of several hundred polygonal corneal facets, a vitreous-like jelly and a "retina", but without nerve fibres.

In STARFISHES (Asteroids such as the common five-rayed *Asterias*), although the skin is often diffusely light-sensitive, on the tip of each of the five arms a visual

¹ Compare iridocytes, p. 89.



Sea-cucumber,
Holothuria



The sea-urchin,
Diadema

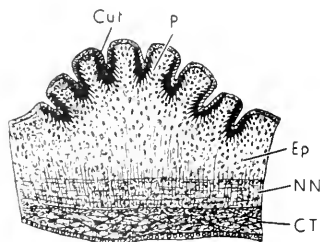


FIG. 167.—The optic cushion of the Asteroid

Cut, cuticle; CT, connective tissue; Ep, epithelium; NN, nerve-net; P, pigment cells.

organ is formed as a modified tube-foot lying on a slight elevation (the "optic cushion") on the dorsal surface of the terminal ossicle (Fig. 166). The organ is bright red due to the presence of β -carotene and esterified astaxanthin and consists of an aggregation of several cupulate ocelli of the simplest type covered by cuticle and lined by sensory and pigmented cells (Plate I; Fig. 167) (Pfeffer, 1901); a central lenticular body may serve to concentrate light upon the receptive elements (van Weel, 1935; Smith, 1937). The optical function of this organ in *Asterias* has been convincingly demonstrated by Hartline and his co-workers (1952) who recorded the electric impulses following stimulation by light. The terminal tube-foot appears to be olfactory in function.

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WORMS

The large group of "WORMS" shows a variety of visual organs as pleomorphic as the multitude of forms which constitute this loose grouping of animals, showing every variation from a unicellular eye to a relatively complex organ. In some cases the surface of the whole body seems to be sensitive to light and it has not been possible to identify specific sensory cells; in most cases, however, specialized sensory structures occur, for the elucidation of which we are largely indebted to the classical work of Richard Hesse (1899-1908). Their presence, their number, and the degree of their differentiation vary with the animal's mode of life. This is the lowest group in the animal kingdom to show bilateral symmetry and the sense organs share in this general scheme of distribution; moreover, these organs are usually concentrated towards the head-end of the animal where they are of greatest biological value.

PLATE I
THE LIGHT-SENSITIVE APPARATUS OF THE STARFISH

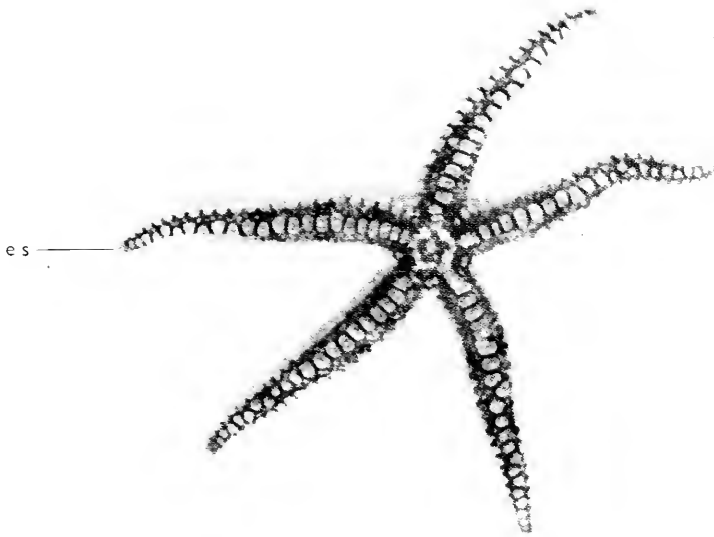


FIG. 1. *Marthasterias glacialis*, showing the position of the eye-spot, *e.s.*, one of which is present at the tip of each of the five arms.



FIG. 2.—The excised eye-spot (optic cushion) showing the optic cups, *o.c.* They have a striking red colour due to *β*-carotene and esterified astaxanthin; it is to be noted that some of the colour of the body-wall, which is also light-sensitive, is due to the same pigments (N. Millott, *Endeavour*, 1957).

These photoreceptors are of the most varied types and many species possess eyes of more than one variety. The neuro-sensory cells may be either apolar in type provided with an internal optic organelle, or bipolar, provided with a ciliated or striated border¹; they may occur as single cells or in groups forming an eye of either the subepithelial or epithelial variety, in which case it may show a flat, cupulate or vesicular arrangement. Pigment is a constant association, situated within the sensory cells or in special supporting cells. If a refractive medium is present it may be formed either from the retinal or the epidermal cells, while light-refracting structures are usually cuticular in origin. As a general rule their function can only be the primitive ability to detect light, but the visual organs of some types, such as some polychaete worms, are structurally capable of some degree of localization and resolution (a *directional eye*) and perhaps even of visual imagery.

UNSEGMENTED WORMS

The unsegmented worms may be divided into three phyla—flat-worms, ribbon-worms, and thread-worms.

1. PLATYHELMINTHES or FLAT-WORMS constitute a group of very simply organized creatures the members of which show the progressive degeneration associated with parasitism. It is divided into 3 main classes:

(a) TURBELLARIANS, freely-swimming leaf-shaped aquatic creatures of carnivorous habit, frequenting brackish or salt water or moist places on land; the name is derived from the turbulence caused in the water by the beating of their cilia when they swim. They are classified according to the arrangement of the gut—the minute marine *Acoela* (without intestine), the small salt and fresh-water *Rhabdocoela* (rod-shaped intestine), the (mainly) marine *Allocoela* (irregular intestine), the small, flat, elongated *Tricladida* (3-branched intestine) found in fresh or salt water or on land (including the *Planaria*), and the large, leaf-like, marine *Polycladida* (many-branched intestine).

(b) TREMATODES or FLUKES, leaf-like parasites, external or internal, found on or in all types of Vertebrates, clinging to their hosts with suckers. Examples are the liver-fluke, *Fasciola hepatica*, which infests the livers of sheep and cattle, or the *Schistosoma haematobia* which causes bilharziasis.

(c) CESTODES or TAPE-WORMS, endoparasites, frequenting the alimentary canal of Vertebrates, including domestic animals and man, such as *Tania echinococcus*, or *T. solium*.

2. NEMERTINES or RIBBON-WORMS, ribbon- or thread-like in shape, often vividly multi-coloured, varying in size from under an inch to enormous lengths (25 metres in *Lineus*) and provided with cilia and a remarkable retractile proboscis forming a tactile organ used to capture prey. Most are marine in habitat, creeping in the mud and under stones; a few are found in fresh-water (*Prostoma*); some are terrestrial (*Geonemertes*); and a few live commensally with bivalves or ascidians.

3. NEMATODES, ROUND- or THREAD-WORMS, cylindrical in shape and often minute, which teem in the soil or in water and are often endoparasitic in plants and animals (*Ascaris*, *Trichinella*, *Ankylostoma*, *Filaria*, etc.); but free-living forms occur at any rate in part of the life-cycle.

¹ p. 127.



Polyclad,
Leptoplana



Schistosoma



Tania
echinococcus

The PLATYHELMINTHES have sense organs only of the most rudimentary type—if any. The freely-living TURBELLARIANS (Planarians, etc.) are the most adequately equipped with eyes (Figs. 168 to 170). These may be merely two or four in number, in which case they lie on the dorsal aspect of the head-end associated with the tentacles near the cerebral ganglion, as in the fresh-water Rhabdocœla; but others such as the marine Polycladida may possess several hundred. A common arrangement, well seen in the Tricladida, is that these multiple ocelli are distributed around the circumference of the body concentrated particularly at the anterior margin (Figs. 168 and 170) (Busch, 1851; Hyman, 1938–51). The eyes are always very elemen-

FIGS. 168 TO 170.—THE EYES OF TURBELLARIAN WORMS.

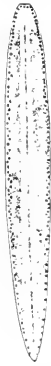


FIG. 168.—A land planarian, *Geoplana mexicana*.

There is a row of eyes along the entire margin of the animal (after Hyman).

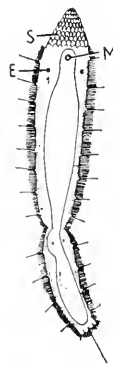


FIG. 169.—The eyes of the pelagic Rhabdocœle, *Alaurina proliferata*.

S, papillated snout; M, mouth; E, paired eye (after Busch).

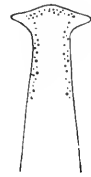


FIG. 170.—The eyes of the fresh-water planarian, *Polycelis coronata*. They are concentrated at the head-end (after Hyman).



Dendrocoelum

tary, and lacking a dioptric apparatus are capable only of light perception although a directional appreciation may be evident (Taliaferro, 1920). The number of visual cells is said to vary between 1 and 200 (Hesse, 1896; Schmidt, 1902). Occasionally, as in *Dendrocoelum*, they are of the flat epithelial type (Fig. 95). Usually they are of the subepithelial type, appearing as minute pigmented spots about 0.1 mm. in diameter and consisting of a pigmented goblet enclosing the sensory cells (Figs. 91 and 92). In these the sensory cells are of the bipolar type with a striated margin facing away from the direction of light to form an inverted retina. When the eyes are near the cerebral ganglion the sensory fibres enter the latter directly; otherwise they enter the peripheral nerve-net.

In some Rhabdocœla (*Stenostomum*) curious hemispherical bodies consisting of refringent granules lying underneath a bowl-shaped mass have been credited with a photosensitive function; there is no good evidence, however, for this assumption.

Eyes are lacking in the cave-dwelling planarians (Kenkiidæ) and in endoparasitic Rhabdocœla.¹

TREMATODES may possess simple ocelli in the larval stage (as in the liver-fluke, *Fasciola hepatica*), but the adults, leading an essentially parasitic existence, rarely possess sense organs. If they are present they are of the simplest type, usually consisting of a single cell with a striated border invested by a cup of pigment (Hesse, 1897; André, 1910; Faust, 1918); a typical example is seen in the unicellular eye



Fasciola hepatica

FIGS. 171 AND 172.—THE EYES OF NEMERTINE WORMS.



FIG. 171.—*Lineus ruber*.
E, eyes (after Hyman).



FIG. 172.—The head of *Amphiporus angulatus*. E, eyes (after Hyman).

of *Tristomum papillosum*, a marine Trematode parasitic on fishes (Fig. 87).

CESTODES, in keeping with their endoparasitic life, are without sense organs.²

Among the NEMERTINES, most of which are freely-living and marine in habitat, rudimentary eyes of the same subepithelial type as occur in flat-worms are general and occasionally are very numerous (Figs. 171-72). They are always limited to the anterior end of the animal. Some species possess two eyes, others four or six on the prostomium; others up to 250 eyes (*Amphiporus*) arranged in clusters or rows, while the number may vary in different individuals of the same species. The eyes are nearly always subepithelial in type consisting of bipolar cells terminating in a brush border enclosed within a pigment cup of epithelium (Hilton, 1921) (Fig. 93). The eyes of the terrestrial genus,



Amphiporus

¹ pp. 724, 733.

² p. 734.

Geonemertes, differ from the usual type. In these the pigmented epithelium forms a complete circle within which is a mass of refractile material ; the nuclei of the sensory cells are arranged outside the circle of pigment and their distal terminations pass through it into the central refractile mass (Schröder, 1918).

In the NEMATODES, the majority of which are endoparasitic, sense organs are limited to papillæ on the lips ; in the free-living sexual state, however, rudimentary eyes may exist, consisting of a lens-like cuticular body resting on a cup of pigmented cells (Steiner, 1916 ; Hilton, 1921 ; Schulz, 1931).

Nematode,
Ascaris



SEGMENTED WORMS (ANNELIDS)

The segmented worms exhibit much diversity in habit and structure but their essential characteristics are segmentation of the body with paired appendages on each segment and a closed vascular system. Annelids are found both in marine and fresh water and on land, and in the entire phylum more than 6,500 species are known. These are divided into 4 classes, the first two of which are provided with chitinous bristles or setæ for locomotion.

1. OLIGOCHÆTES (with few setæ), hermaphroditic creatures, essentially terrestrial in habit, typified in the common earthworm, *Lumbricus terrestris*, or the tiny aquatic mud-worms living in brooks or between tide-marks.

2. POLYCHÆTES (with many setæ), essentially marine in habit ; in them the sexes are separate. Two types exist, distinguished by their habits. The more active forms (ERRANTIA) are typified in the common lob-worm, *Arenicola marina*, found burrowing in sandy beaches, or the freely-swimming types, such as the rag-worm, *Nereis*. The sedentary forms (SEDENTARIA) are tubicolous in habit leading a sluggish life within tubes, limy, sandy or gelatinous ; as an adaptive characteristic the tentacles, gills and sensory organs are aggregated in the anterior part of the worm which protrudes from the tube.

3. ARCHIANNELIDS comprise a small and anomalous class of simple marine worms with juvenile characteristics and without setæ, freely swimming or burrowing in sand and gravel.

4. HIRUDINES or LEECHES form a highly specialized and much modified class, most of which live in fresh water in ponds or sluggish streams although a few are marine and others (the wiry land-leeches of the Far Eastern jungles, *Hæmadiipsa*) are terrestrial, living in moist places. In habit they are greedily suctorial, sucking the blood of fishes, amphibians or other victims.

Arenicola



Hæmadiipsa



Eyes are usually lacking in the OLIGOCHÆTES ; of those possessing visual organs, the most typical example is the earthworm, *Lumbricus terrestris*. Its unicellular light-sensitive organs distributed in the epithelium and aggregated around subepithelial nerves have already been fully described ¹ (Figs. 86, 88). These visual elements are situated where they are of the greatest biological value, being concentrated at the two extremities, particularly the anterior.

Lumbricus



¹ p. 131.

Thus W. N. Hess (1925) found that in the prostomium there were some 440 light-sensitive cells in the epidermis and 700 situated in nearby nerve enlargements, while in subsequent segments they were much fewer. Their relative numbers in corresponding small areas ($200 \times 300\mu$) on the dorsal surface of the animal are as follows—in the prostomium, 18; 1st segment, 10; 2nd segment, 5; 3rd segment, 3; 40th segment, 0; antepenultimate segment, 1; penultimate segment, 1; last segment, 4. The segmental photic sensitivity varies directly with the number of receptors, and the distribution of light-sensitive elements conforms with the habits of the earthworm.¹

Among POLYCHÆTE WORMS, the burrowing lob-worm, *Arenicola marina*, is not provided with visual organs although the prostomial

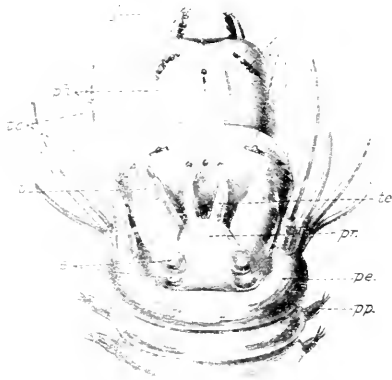


FIG. 173.—THE HEAD OF *NEREIS*, SHOWING THE FOUR EYES.

e, eyes; *j*, jaw; *p*, palp; *pe*, peristomium (first two segments fused); *ph*, pharynx; *pp*, first ordinary parapodium; *pr*, prostomium; *t*, accessory teeth; *tc*, tentacular cirri; *te*, tentacle. (From Borradaile's *Manual of Elementary Zoology*; Oxford University Press.)

lobes are diffusely sensory. In contrast with the burrowing type, however, the freely-swimming marine polychaetes show a much richer development (Fig. 173). Of these, *Nereis* is a typical example. This worm has four prominent eyes situated on the prostomium, each of the cupulate type with a cuticle externally and a retina internally formed of well-developed sensory cells with rod-like receptor endings (Fig. 101). Other forms, such as *Polyopthalmus*, have in addition to the prostomial eyes similar pairs of subepithelial organs in many segments of the body: such eyes² are formed sometimes on each segment (*Myxicola aesthetica*; *Eunice*), and occasionally on the anal segment (*Fabricia*).

A much more complex type of eye of the vesicular type is found



Nereis

¹ p. 572.

² These organs, usually considered to be "eyes" are said by some to be light-producing (p. 736) (Benham, 1896).

in certain pelagic polychaetes such as *Alciopa* and *Eupolyodontes*, the intimate structure of which has already been described.¹ These worms have two eyes, sometimes facing forwards (*Eupolyodontes*), sometimes diverging widely (*Alciopa*) (Fig. 174). Each organ is provided with

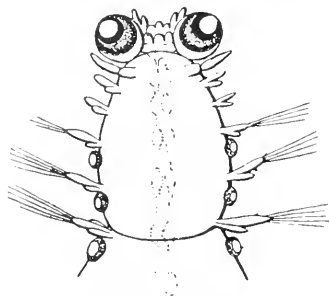


FIG. 174.—THE ANTERIOR END OF THE POLYCHÆTE WORM, *ALCIOPA*.

Showing the two large eyes (after Greeff).



Branchiommata

an elaborate retina, a lens, an accommodative mechanism and extra-ocular muscles suggesting the potentiality for binocular vision, an equipment which seems capable of considerable visual powers approximating those of the Cephalopods.² Little, however, is known of the habits of these worms.

In the sedentary tubicolous polychaetes (*Potamilla*, *Branchiommata*, *Dasychone*, etc.) the ocelli are frequently grouped in masses on the branchial filaments to form a composite simple eye of great complexity (Brunotte, 1888 ; Andrews, 1891 ; Hesse, 1896) (Figs. 175 and 176) ; *Vermilia infundibulum* has at least 220 ocelli on the external aspect of each branchium, a total of some 11,000 eyes (Parker and Haswell, 1940). These creatures live within their tubes from out of which extend the branchial plumes bearing the filaments on each of which there is one or more such eyes (Figs. 128, 129). The curious thing, however, is that in

FIGS. 175 AND 176.—THE COMPLEX EYES OF TUBICOLOUS POLYCHÆTES.

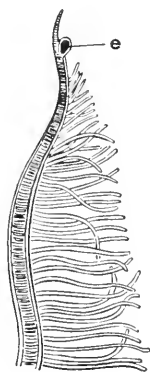


FIG. 175.

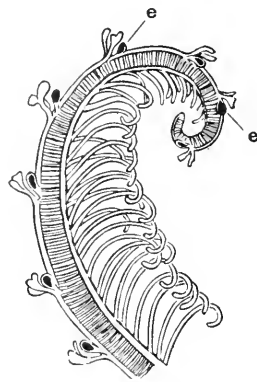


FIG. 176.

The secondary filaments are seen issuing horizontally from the central axis of the branchial filament. Fig. 175, *Branchiommata*, showing the single complex eye, *e*, near the termination of the central axis. Fig. 176, *Dasychone*, showing the row of complex eyes (2 of which are marked *e*) running up and down the central axis (after Benham, *Camb. Nat. Hist.*).

¹ p. 143.

² Fig. 112.

Branchiomma, at any rate, these structures do not seem to be essential for the most characteristic responses of the worm to changes in the intensity of light (Millott, 1957); the position is therefore somewhat anomalous.

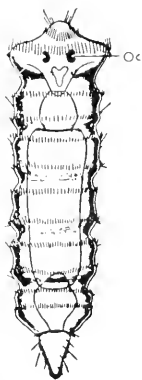


FIG. 177.—THE ARCHIANNELID, *DINOPHILUS*.

Showing the paired ocelli, Oc (after Sheldon-Harmer).

In the simple marine ARCHIANNELIDS, eyes of a similar type are found. In *Dinophilus*, for example, a minute worm found among algae, two kidney-shaped pigmented eyes are found on the prostomium (Hilton, 1924) (Fig. 177).

LEECHES (HIRUDINEA) may be provided with visual organs of a simple type varying in number from 2 to 10 (Hesse, 1897; Herter, 1932); they are incapable of optical imagery although highly light-sensitive, but in some species may be absent. They are found near the anterior extremity of the body and vary considerably in their morphology, but the visual cells are always of the spherical apolar type with a central optic organelle (Figs. 178–9).

In *Branchellion* these organs are unicellular; in *Piscicola* they consist of 12 cells arranged in a row surrounded by pigment. In *Hæmopsis* both unicellular and multicellular ocelli are found (Fig. 179). In the common medicinal leech, *Hirudo medicinalis*, there are segmental papillæ with a sensory function on the middle ring of each of the 26 segments. Although all the sense organs are serially homologous the pairs on the dorsal surface of the first five segments are purely visual, constituting ten “eyes” (Fig. 90), provided with a rich nerve supply to the cerebral ganglia. At the other extremity the



Branchellion



Hirudo

FIGS. 178 AND 179.—THE EYES OF LEECHES.

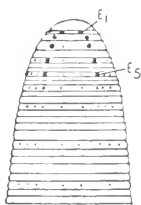


FIG. 178.—The head end of the medicinal leech, *Hirudo medicinalis*.

The dorsal aspect. The body is divided into segments, each of which contains 5 rings (annulæ). In the middle ring of each segment the segmental papillæ have a sensory function. The first 7 (and the last 3) segments have less than the normal number of rings, and the first 5 show two paired eyes as larger black spots, E_1 to E_5 , serially homologous with the sensory papillæ (see Figs. 89–90) (after Parker and Haswell).

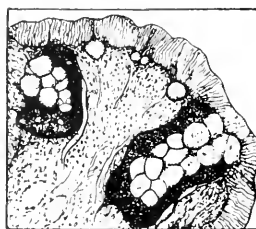


FIG. 179.—Solitary and aggregated eyes of the horse-leech, *Hæmopsis sanguisuga* (after Kappers).

organs are probably purely tactile, and between these two regions the sense organs are compound since they contain both visual and tactile cells (Fig. 89).¹

Subsidiary Invertebrate Phyla

For convenience, four small and subsidiary phyla of the Invertebrates are most usefully considered here.



Chaetognath,
Sagitta

CHÆTOGNATHA ("bristle-jawed") or ARROW-WORMS, delicate, translucent torpedo-shaped creatures comprising some 30 species which swim in incredible numbers in great shoals among the plankton of all seas, have well-developed eyes. *Spadella*, for example, or *Sagitta*, has two composite simple eyes at the anterior extremity of its body, formed by the union of 5 ocelli, the structure of which has already been described (Fig. 132); although presumably tripartite, the nerve fibre from each eye is gathered into a single optic nerve trunk.

FIGS. 180 AND 181.—THE EYES OF ROTIFERA.



FIG. 180.—The cerebral eye.

Section through the cerebral ganglion of *Synchaeta*, showing two cerebral eyes, E (after Peters).

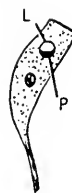


FIG. 181.—The frontal eye.

The eye of *Rhinoglena* with pigment spot, P, and refractile lens, L (after Stossberg).



Rotifer

ROTIFERA ("wheel-bearers"), the beautiful minute wheel-animalcules, sometimes of fantastic shape, which swim so abundantly with the aid of a crown of cilia like revolving wheels in fresh water, damp moss or the sea all the world over, are usually highly light-sensitive. There is a generalized dermatoptic sense which evokes a positive phototaxis, but exact orientation is determined by the eyes and varies with their morphological development (Viaud, 1938-43). Frequently there is a single or paired CEREBRAL EYE embedded in the dorsal nerve ganglion (*Synchaeta*) (Fig. 180). In other species, sometimes in addition to the cerebral eyes, there is one or two frontal or lateral eyes (Fig. 181). The cerebral eye consists of a single cell resembling a brain cell; the lateral or frontal eyes are epidermal cells inside which is a lens-like body associated with a mass of red pigment (Peters, 1931; Stossberg, 1932). *Branchionus*, one of the commonest members of this class which inhabits ponds and ditches in abundance, has a simple unpaired eye surrounded by red pigment and associated with tufts of sensory hairs, situated where the cerebral ganglion comes into contact with the body-wall just behind the wheel of cilia at the anterior end of the animal.



Bryozoa

POLYZOA (BRYOZOA), very ancient plant-like organisms which include freshwater and marine forms (sea-mats, etc.) are sessile colonial corallines or "moss animals" which grow in tufts on the shores or in pools all over the world encrust-

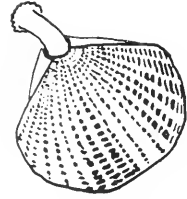
¹ p. 133.



FIG. 182.—THE OCELLI (Oc) OF THE LARVA OF THE BRACHIOPOD, *CISTELLA* (after Gladstone).

ing seaweed, rocks and piles with a lace-like coating, and multiply by budding. Some 1,800 species have been described. The larvæ of some species during their short freely-swimming life before they settle on the rocks or mud, are sometimes provided with rudimentary eyes. Thus the larvæ of *Bugula turrila* which have 4 or 5 slender flagella, have 4 brilliantly red spherical eye-spots, 2 close to the pyriform organ and 2 larger eye-spots located in the opposite hemisphere. The larva of the American *Bugula flabellata* has no light-sensitive organs, but the European variety has 10 symmetrically arranged eye-spots (Nitsche, 1870; Calv t, 1900; Grave, 1930; Lynch, 1949).

BRACHIOPODA (LAMP-SHELLS), marine organisms of great antiquity which have existed unchanged since the Palæozoic era¹ and are found in the seas in most parts of the world covered by their shells firmly attached to rocks, are in some cases devoid of sense organs; in the freely-swimming larvæ of others, patches of sensory epithelium form paired eye-spots immediately over the cerebral ganglion which disappear when the larvæ become sessile (*Cistella*) (Fig. 182); but rudimentary eyes are exceptional (*Megerlia*).



Brachiopod

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MOLLUSCA

Among MOLLUSCS ("soft bodied") the most elementary types of eyes are found and also the most elaborate forms that the simple eye assumes, organs capable of a degree of resolution that the animal cannot probably utilize: between the two extremes almost every imaginable form of eye is encountered. The characteristics of this phylum are an unsegmented body with a muscular "foot" protruding

¹ *Lingula*, with fossil records dating some 500,000,000 years, is the oldest known animal genus.



Solenogastre



Nudibranch

Pulmonate,
Limnaea*Nautilus*

from the ventral surface serving for locomotion, a dorsal or lateral fold of the body-wall to form a mantle or pallium within which lie the gills, and frequently a shell. As a general rule, two cephalic eyes subserve the visual function, but these may be replaced by more rudimentary organs in the dorsal region or around the margin of the mantle or at the end of the tentacles or the siphons. Occasionally eyes are lacking, in which case the skin has usually some sensitivity to light.

The large phylum of Molluscs is conveniently divided into six classes; three are relatively unimportant, sluggish in habit, and live in the mud or sand of the sea-bottom—the shelled PLACOPHORANS and SCAPHOPODS, and the worm-like SOLENOGASTRES. The remaining three classes contain an enormous number of species of great variety—Gastropods, Lamellibranchs (Bivalves) and Cephalopods.

The GASTROPODS (“belly-footed”) constitute a very varied group comprising some 40,000 species and include three main classes:

(a) OPISTHOBANCHS: sea-hares, Pteropods (transparent marine plankton forms), and the brilliantly coloured Nudibranchs or sea-slugs which have no shell;

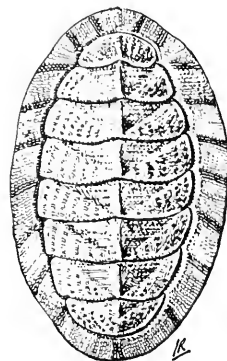
(b) PROSOBANCHS, an enormous and varied group including sea-snails, whelks, limpets, Heteropods, etc.;

(c) PULMONATES. The abundant and universally distributed fresh-water and terrestrial snails and slugs.

The BIVALVES: shell-fish such as cockles, mussels, clams, scallops and oysters which live within a rigid hinged shell often at the bottom of the sea. They comprise some 11,000 species.

The remaining class, the CEPHALOPODS, are the most interesting; they are usually active, moving by jet propulsion with a jet of water expelled from the siphon. Two orders are recognized: the Tetra-branchiates, with two pairs of gills, represented by a single living species, the Pearly Nautilus of the South Pacific, and the Dibranchiates, with a single pair of gills and remarkably well-developed eyes (cuttlefish, squid, octopus).

In the most primitive type of molluscs, the PLACOPHORANS, eyes may be lacking although some of their sensory organs may be sensitive to light (Plate, 1899; Nowikoff, 1907). Some of them possess a multitude of minute ocelli; *Corephium*, for example, may have as many as 8,500. The most interesting in this class are the Chitons (“coats-of-mail”); these possess cephalic eyes in the larval stage which, however, disappear as the adult becomes clothed by its eight-plated dorsal shell, thus rendering them useless. In place numerous innervated papillae appear containing sensory organs (*aesthetes*) which perforate the shell, appearing in rows as minute black dots (“shell-eyes” (Looseley, 1884) (Fig. 183). The larger of these

FIG. 183.—THE MOLLUSC,
CHITON.

The sense organs, *aesthetes*, perforate the shell, appearing as minute black dots; the larger of these contain an ocellus (Thomson's *Zoology*, James Ritchie; Oxford University Press).

are light-sensitive, containing an ocellus composed of a deep retinal cup surrounded by pigment lying beneath a lens, the whole organ being covered by a cornea. It is to be remembered, however, that Crozier (1920) could find merely a general photosensitivity in *Chiton*, most pronounced where ocelli are lacking. Among SOLENOGASTRES, these organs are replaced by simple epithelial papillae. In the SCAPHOPODA ("tusk-shells"), a small class of molluscs which burrow in the sand (*Dentalium*, elephant's-tooth shell, etc.) the sensory organs are represented only by statocysts.

Most members of the large class of GASTROPODS, the eyes of which were studied at an early date by J. Müller (1831), are provided with ocelli of a relatively primitive kind often associated with the tentacles. In the extremely passive limpet, *Patella*, the eyes at the base of the tentacles are very elementary, being merely represented by simple



Dentalium

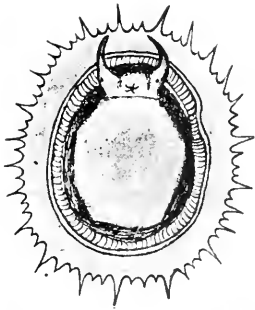


FIG. 184.—THE LIMPET, *PATELLA VULGATA*

Ventral surface. Note the simple eyes (appearing as black dots) at the base of the 2 tentacles. The star-shaped median structure is the mouth (Thomson's *Zoology*, James Ritchie; Oxford University Press).

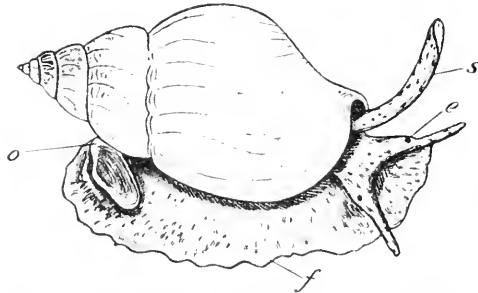


FIG. 185.—THE COMMON WHELK OR BUCKIE, *BUCCINUM UNDATUM*.

Note the two simple eyes (*e*) at the base of the tentacles. *s*, respiratory siphon; *o*, operculum; *f*, foot (Thomson's *Zoology*, James Ritchie; Oxford University Press).

cupulate depressions of sensory and pigmented cells (Figs. 97 and 184). More usually, however, the eyes are vesicular in type. These are typified in the two simple vesicular eyes of the grey slug, *Limax*, or the snail, *Helix* (Fig. 110), perched on the tips of the two longer (and posterior) tentacles ("horns") and innervated from the cerebral ganglion (Galati-Mosella, 1915); on exposure to light the tentacle is capable of retraction like the finger of a glove so that the eye can be drawn within it (Figs. 186 to 188). The common whelk, *Buccinum*, has eyes of a somewhat similar vesicular type situated near the base of the tentacles (Fig. 185), as also has *Murex*.



Limax



Shell of *Murex*

The most elaborate eye of this type, however, is seen in the spider-shell, *Pterocera lambis*, a gastropod found in quantity on tropical reefs. According to

THE EYE IN EVOLUTION

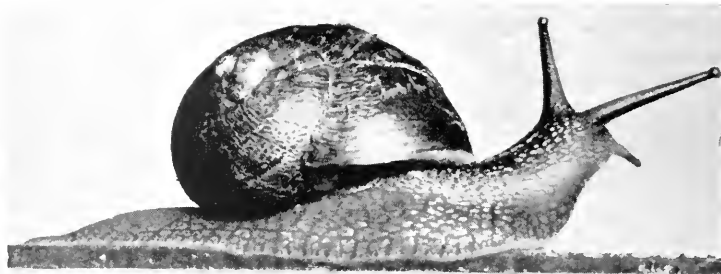
FIGS. 186 TO 188.—THE COMMON GARDEN SNAIL, *HELIX ASPERSA*.

FIG. 186.—The two eyes are situated on the tip of each of the long posterior horns.



FIG. 187.—The eye at the tip of the expanded horn.

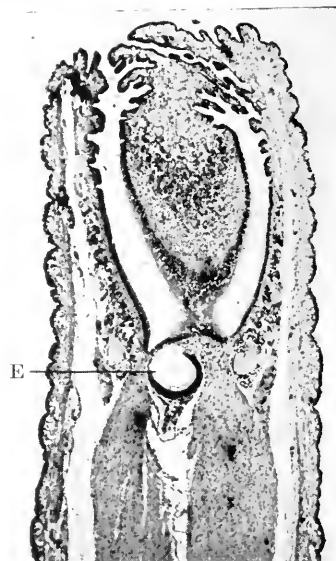


FIG. 188.—The eye (E) retracted into the horn. The horn invaginates like the intumed finger of a glove; the obliquity of this section gives the appearance of a double cavity (Norman Ashton).

Shell of *Pterocera*

Prince (1955), the two vesicular eyes, which have an elaborate neural structure,¹ are mounted on the tip of stalks (ommatophores) which also carry an olfactory tentacle and a sensory node (Fig. 189). These, supplied with muscles arranged around a central sinus, are retractile partly by muscular activity and partly by engorgement by haemolymph. Retraction can be slow and voluntary or rapid and reflex in response to stimuli such as touch, odour or the cutting off of the reaction is thus the opposite of that seen in the snail. It appears that at a certain amount of convergence upon an object is possible.

¹ p. 142.

In *Onchidium*, a naked littoral Pulmonate which creeps on rocks near the high-water mark, a unique type of vesicular eye with an inverted retina is found arranged on papillæ scattered over the skin of the back in groups of six or up to a total which may reach a hundred (Fig. 122).¹

An interesting elaboration is seen in some marine HETEROPODS (*Carinaria*,



Carinaria

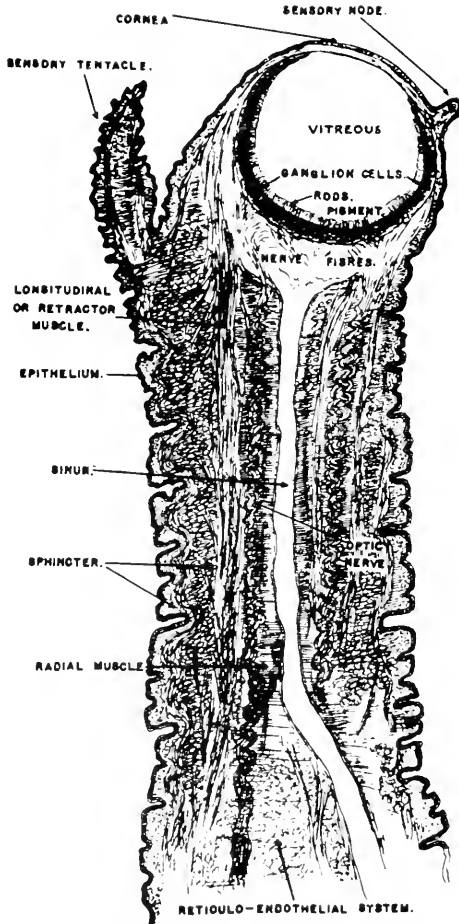


FIG. 189.—THE STALKED EYE OF THE SPIDER-SHELL, *PTEROCERA LAMBIS*.

Showing the sensory tentacle, sensory node, sinus, and muscular systems (after J. H. Prince).

Pterotrachea) which have tubular eyes containing a large spherical lens; the available visual field is increased by the provision of lateral "windows" wherein pigment is lacking, opposite which the posterior retina is prolonged up the side of the eye. *Pterotrachea coronata* which swims with its belly in the air has an eye at the extremity of each of its two tentacles; images in front are focused on the posterior retina by the enormous lens, while movements and changes in

¹ p. 148.

illumination above and below are probably appreciated through the dorsal and ventral "windows" (Hesse, 1908 ; v. Hess and Gerwerzhagen, 1914). Such fenestrated eyes are also seen in abyssal fishes.¹

LAMELLIBRANCHS or BIVALVES have an undeveloped head-region, and the two lobes of the mantle which secrete the two valves of the shell are frequently united posteriorly to form exhalant and inhalant siphons. Anterior eyes are therefore rare. Such cephalic eyes are sometimes seen in larval forms but in the adult they tend to become vestigial remnants, a cupulate depression of bipolar sensory and



Aricula



Mytilus

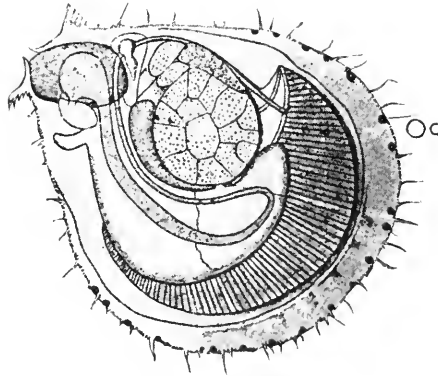


FIG. 190.—THE COMMON SCALLOP, *PECTEN*.

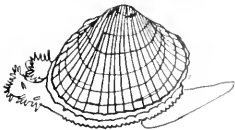
The pallial ocelli, Oc, are seen in a single row round the margin of the mantle. For section of the eye, see Fig. 123 (after Pelseneer).

pigmented cells as occurs in the pearl-oyster, *Aricula*, or the edible mussel, *Mytilus*. More usually they are replaced by ocelli located in situations where they are of greater biological value such as the siphons, the tentacles or the mantle (Fig. 190).

Thus the ocelli are found on the inner surface of the siphons in clams which habitually lie buried in the sand or mud (*Mya*) or bore into soft rocks (*Pholas*) (Light, 1930) ; as they lie buried these molluscs extend the siphon to the surface to feed and at daybreak or whenever the illumination increases the siphon is withdrawn (Wenrich, 1916 ; Hecht, 1919-20 ; Piéron, 1925 ; Folger, 1927 ; and others). It will be remembered that these visual organs are of the most simple type resembling those of the earthworm, being merely single cells of the apolar type with a refractive organelle in the cell-body richly supplied with nerves.² In the cockle, *Cardium*, small ocelli are situated at the tips of the tentacles, about 100 in number, which are arranged around the siphonal apertures ; the eye is of a simple cupulate form, the cup-shaped retinal cells resting on a layer of double pigmented cells underneath a large ectodermal cornea, the lens and cornea (Kishinouye, 1894). As in the pallial eyes of *Pecten*, the cornea is inverted.



Pholas



Cardium



Pecten

¹ p. 323.

² p. 131.

Most bivalves, however, have numerous ocelli arranged like a coronet around the margin of the mantle (PALLIAL EYES); these may be numbered in hundreds and are probably to be looked upon as modified tentacles. In some forms, such as *Lima*, they are very primitive. This bivalve is provided with 30 simple cup-shaped depressions, 0.3 mm. in diameter, lined with sensory and pigmented cells forming primitive cupulate eyes; in others such as the fresh-water mussel, *Anodonta*, eyes are completely absent. Most of these types are relatively sluggish and quiescent, but in actively swimming forms the eyes may be more elaborate. This development is well exemplified in such bivalves as the common scallop, *Pecten*, and *Spondylus*, both of which possess eyes unique among Molluscs. The pallial eyes are arranged in a single row around the edge of the mantle; when they are exposed as the shell gapes they shine as brilliant emerald green or purple spots, 0.6 to 0.8 mm. in diameter; 28 to 46 have been counted in the upper half of the mantle, 15 to 36 in the lower, and each is borne on a contractile pedicle (Fig. 190). These are of remarkable complexity with a well-formed inverted retina which appears to be much more elaborate than the visual demands of the shell-fish would seem to warrant (Fig. 123). Each is connected by means of its optic nerve with a large circumpallial nerve and so with the branchial ganglion.¹ An anomalous occurrence in certain lamellibranch molluscs (the Noah's-ark shell, *Arca*; *Pectunculus*), is that of unicellular ocelli grouped together in a spherical mass constituting an aggregate eye which bears a superficial resemblance to a compound eye² (Carrière, 1885; Patten, 1886; Hesse, 1900).

The CEPHALOPODS (cuttlefish, etc.) usually exhibit the most elaborate visual organs found among Molluscs, a characteristic understandable in view of their active behaviour and carnivorous habits; only one species living at abyssal ocean depths is known to lack eyes, *Cirrothauma murrayi*.³ They are the most specialized of the molluscs and present considerable diversities of type, but most of them are freely swimming and they all have a well-developed head furnished with numerous "arms" bearing tentacles or suckers and provided with eyes and other sensory structures.

In the pearly nautilus of the seas of the Far East, the sole survivor of the primitive and almost extinct tetrabranchiate Cephalopods which were largely Palaeozoic in distribution, the eye retains its ancestral simplicity and consists merely of an epithelial depression with a tiny aperture 2 mm. in diameter (Figs. 100 and 191); it is situated on a raised flat peduncle which is also provided with two "ocular tentacles", probably olfactory in function.

In the more recent and voraciously carnivorous dibranchiate Cephalopods, however, such as the common cuttlefish, *Sepia*, the



Anodonta

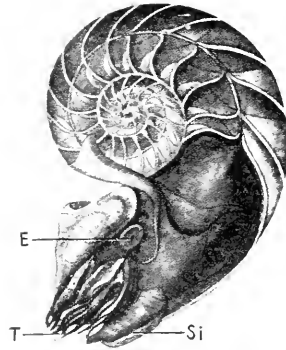


FIG. 191. — THE PEARLY NAUTILUS, *NAUTILUS POMPILIUS*.

The animal is seen in section. Above is the spiral shell. E, the eye, which opens to the exterior; Si, siphon; T, tentacles (after Owen).



Spondylus



Sepia

¹ p. 527.

² p. 151.

³ p. 723.

squid, *Loligo*, and the octopus, the two eyes are large and prominent (Figs. 192-3). They are situated conspicuously on either side of the head behind the main body of tentacles, protected in part by the cartilage surrounding the brain and in part by cartilages in their own



FIG. 192.—*OCTOPUS VULGARIS* (J. Z. Young).

walls, and provided with rudimentary lids and a set of 4 extra-ocular muscles which confer a wide range of movement on the globe (Hesse, 1908 ; Tompsett, 1939) (Figs. 113 and 114). The complex structure of these organs has already been described,¹ and although they rival the

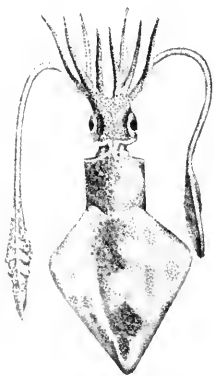


FIG. 193.—THE COMMON SQUID, *LOLIGO VULGARIS*.

Show the two large prominent eyes, one on each side of the head (after K. ... in).

eyes of Vertebrates in their morphology, they are simple in type, derived from the epithelium. The close resemblance of the eyes of these molluscs to the cerebral "camera" eyes of Vertebrates is a striking example of convergent evolution whereby Nature achieves comparable results by travelling along entirely different routes. The nervous connections are prominent ; in the posterior wall of each eye is a large optic ganglion from which the thick optic lobes lead directly to the closely associated cerebral ganglion² (Fig. 698). There is a well-developed olfactory sac behind each eye as well as two statocysts and organs of general sensation, but it would seem that vision plays a dominant part in the behaviour of the animal.³

¹ p. 143.

² p. 528.

³ p. 575.

Anomalous types of eyes are seen among Cephalopods found at great ocean depths (Chun, 1903). Stalked eyes comparable to those found in some deep-sea fishes, are exemplified in *Bathothauma* (Fig. 194) and *Sandalops* (Fig. 195): both of these live at great depths in the South Atlantic and the eyes of the latter are unique in that they point obliquely downwards, a curious configuration said to be explained by the fact that the squid swims with its body slanting upwards.

FIGS. 194 TO 196.—THE EYES OF DEEP-SEA CEPHALOPODS.



FIG. 194.



FIG. 195.

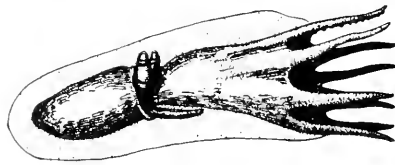


FIG. 196.

FIG. 194.—The deep-sea squid, *Bathothauma*. There are luminous organs beside the eyes which are perched on the end of stalks. Found at a depth of 3,000 m. (from the *Valdivia* Reports).

FIG. 195.—The deep-sea squid, *Sandalops melancholicus*. The stalked eyes are unique in that they point obliquely downwards, possibly because the animal swims with its body slanting upward (from the *Valdivia* Reports).

FIG. 196.—The pelagic octopus, *Amphitretus*. The tubular eyes point upwards and the whole body, including the eyes, is covered with a delicate gelatinous covering (from the *Valdivia* Reports).

Another curious arrangement is seen in *Amphitretus* (Fig. 196) found in the Indian and Pacific oceans. The eyes of this octopod resemble the tubular organs of some deep-sea fishes,¹ pointing directly upwards and enclosed, as is the entire body of the animal, in a delicate and transparent gelatinous covering.

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¹ p. 322.

ARTHROPODA

ARTHROPODS embrace more than three-quarters of the known species of animals, and in view of their number and variety and the diversity of their habits, it is not surprising that an extraordinary variation occurs in their visual organs, while the intense and purposive activity of many of them accounts for the complexity and efficiency of their eyes. Arthropods are characterized by their bilateral symmetry, their segmental structure with jointed appendages, their chitinous cuticle, a distinct head where the sense organs are aggregated, and a nervous system consisting of a dorsal brain-ganglion connected by a ring round the gullet with a double chain of ventral ganglia. From the ocular point of view, although simple eyes often of quite a rudimentary type are frequent, and may indeed be the sole visual organs (as in Arachnids), the characteristic feature of the phylum is the presence of compound eyes of elaborate structure and frequently with highly developed functional abilities.

The Arthropods may conveniently be divided into five sub-phyla :

(1) the primitive worm-like **ONYCHOPHORA**, unique in having a soft, velvety skin, and provided with a separate head, one pair of antennæ and 20 legs all alike ;

(2) the **CRUSTACEANS**, comprising some 25,000 species, with the head fused with the thorax, 2 pairs of antennæ and at least 5 dissimilar pairs of legs ;

(3) the **MYRIAPODS** (centipedes, millipedes, etc.), of some 2,000 species, with a distinct head, one pair of antennæ and numerous legs all alike ;

(4) the **ARACHNIDS**, of some 36,000 species, having 2 body-segments with a fused cephalothorax, without antennæ or wings, and 4 pairs of legs ;

(5) the **INSECTS**, of which more than 577,000 species have now been scientifically described and probably several times as many await investigation, with a body divided sharply into 3 segments, head, thorax and abdomen, bearing one pair of antennæ, 3 pairs of legs and (usually) one or two pairs of wings in the adult.¹



FIG. 197. — THE
ONYCHOPHORE,
PERIPATUS.

Note the two simple eyes on top of the head at the base of the antennæ (Thomson's *Zoology*, James Ritchie, Oxford University Press).

ONYCHOPHORA

The most primitive class of Arthropods, the **ONYCHOPHORA** (*Peripatus* and its allies), inhabiting the forests of the Southern Hemisphere, represent an archaic type, differing widely from other members of the phylum. Seeking out damp places under leaves

¹ In an acre of farm-land in England it has been estimated that there are from 700,000 to 800,000,000 Insects and as many Arachnids. They would usurp Man's domination of the earth were their numbers not kept in check by voracious predators and parasites of their own kind.

and in rotting wood, they are shy and nocturnal in habit with a marked dislike of light. They are beautiful, velvety, caterpillar-like creatures with paired eyes set like diamonds (0·2 to 0·3 mm.) on the side of the head behind the two sensitive antennæ, looking upwards and outwards, not forwards (Fig. 197) ; the eyes, like those of marine Polychætes, are of

FIGS. 198 TO 200.—THE EYES OF THE LARGE CRUSTACEANS (DECAPODS)
(Specimens from Natural History Museum, London).



FIG. 198.

FIG. 198.—The common shrimp, *Crangon vulgaris*. The short eye-stalks bearing the compound eyes lie in sockets in the carapace.

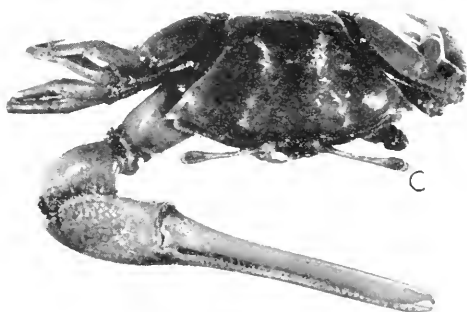


FIG. 199.

FIG. 199.—The fiddler crab, *Gelasimus arcuatus*. There are two compound eyes, C, each standing out prominently on a muscular eye-stalk and protruding on either side of the median rostrum. The left claw is represented by a small stump ; the huge right claw gives the animal its name.

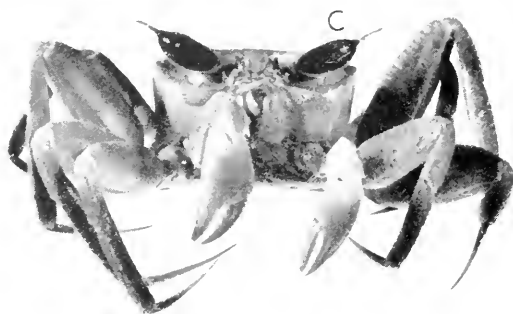


FIG. 200.

FIG. 200.—The racing crab, *Ocypoda ippens*. Two prominent elongated compound eyes, C, are set on eye-stalks, in sockets on the carapace.

the simple type, cupulate in form with a corneal lens formed by the cuticle and hypodermal cells (Fig. 103). Eyes so simple as this serve merely as a means of orientation away from light, and two cave-dwelling species are blind ¹ (Dakin, 1921).

CRUSTACEA

The CRUSTACEANS (lobsters, crabs, shrimps, water-fleas, barnacles, etc.) with few exceptions (land-crabs, wood-lice, sand-hoppers) are aquatic in habit and in most the eyes are prominent; some pelagic forms are transparent except for the eyes which are highly coloured or phosphorescent. Compound eyes are usually present, occasionally supplemented by eyes of the simple type, but in sessile or parasitic forms the visual organs may be vestigial or lacking. Most forms



FIG. 201.—THE WOODLOUSE, *SPHEROMA LANCEOLATA*.

The compound eyes, C, are sessile, lying on the extreme lateral aspects of the head segment (specimen from Natural History Museum, London).



Homarus



Phronima

commence life as a nauplius larva with an oval body, three pairs of limbs and a single eye in the middle of the head.

Of the larger forms (the sub-class MALACOSTRACA) the Decapods (lobsters, shrimps, prawns, crabs) have the most elaborate eyes; of these the common lobster, *Homarus vulgaris*, may be taken as representative. It possesses two typical compound eyes, each with a multitude of ommatidia, associated with the procephalic lobes of the cerebral ganglion. They stand out prominently on muscular eye-stalks to protrude on either side of the median rostrum and are capable of some degree of movement (Fig. 198). In crabs a similar pair of compound eyes with relatively few but large ommatidia are set on eye-stalks in sockets in the carapace (Figs. 199–200). The fact that the eye-stalks in the crab and in the crayfish exhibit optomotor reactions as when they make a small turn or is confronted by a black and white striped rotating disk indicates that their movements are optically determined

¹ p. 724.

(v. Buddenbrock *et al.*, 1954; Dijkgraaf, 1956). One group, the Eryonidea, confined to the deep seas, are blind, the eyes being reduced to stalks only. In other species the eyes are sessile, both in terrestrial Isopods (such as woodlice, Fig. 201) and in pelagic Amphipods: among the latter in the smaller forms the eyes may be minute (*Caprella*, Fig. 202), while in the larger forms they may assume enormous dimensions (the "wondrous-eyed hopper," *Thaumatops magna*, Fig. 203). Sedentary types such as *Asellus*, an Isopod which lives in holes, are completely blind.

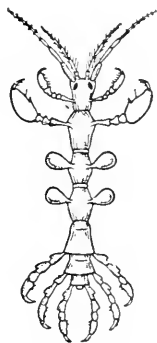


FIG. 202.—THE AMPHIPOD, *CAPRELLA LINEARIS*.

Two ocelli are seen on the dorsal surface of the head.

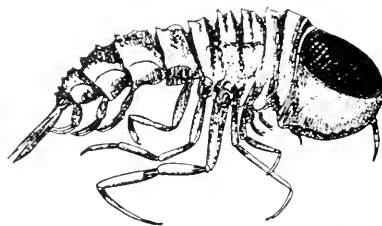


FIG. 203.—THE "WONDROUS-EYED HOPPER," *THAUMATOPS MAGNA*.

The largest known hyperiid Crustacean, found at a depth of 2,500 m., with enormous compound eyes (to the right) ($\frac{3}{4}$ natural size) (after Brehm).

The smaller Crustaceans (branchiopods, copepods, ostracods, cirripedes) include a vast number of types in which the active swimming forms are provided with eyes, while in most sessile and parasitic forms the organs become degenerate. They comprise four diverse and little related orders:

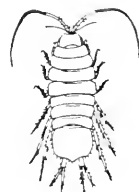
(a) BRANCHIOPODS—protected by a shell and provided with 4 pairs of leaf-like swimming feet. They comprise two groups: (1) the PHYLOPODA such as the brine-shrimp, *Artemia*, which can survive even in Salt Lake, and the large fresh-water *Apus*, of world-wide distribution, and (2) the laterally compressed minute water-fleas (CLADOCERA), *Daphnia*, *Polyphemus* and *Leptodora*, so abundant in fresh water.

(b) OSTRACODS—small laterally compressed creatures with a bivalve shell and indistinct segmentation, breeding parthenogenetically. Typical examples are the fresh-water *Cypris* and the salt-water *Cypridina*.

(c) COPEPODS—elongated segmented creatures without a protective shell. Typical examples are the beautiful fresh-water *Cyclops* and the salt-water *Calanus*. Copepods occur in vast numbers in the seas and constitute the most



Euphausiid
Crustacean



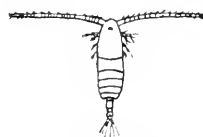
Asellus



Artemia



Leptodora



Calanus

THE EYE IN EVOLUTION



Nauplius larva

abundant animal constituent of the plankton. The group also contains some parasites, as the common fish-louse, *Caligus*.

(d) CIRRIPEDES—with an indistinctly segmented body and usually provided with a calcareous shell. They have a complex life-history. They are born as actively swimming nauplius larvæ, develop into a pupal cypris-like stage, again swimming freely with appendages, but in the adult condition lead an entirely sessile or parasitic life. Typical examples are the barnacle, *Lepas*, which attaches itself to the bottoms of ships or floating logs, the acorn-shell, *Balanus*, which

FIGS. 204 TO 206.—THE EYES OF SMALL CRUSTACEANS
(Specimens from Natural History Museum, London).



FIG. 204.

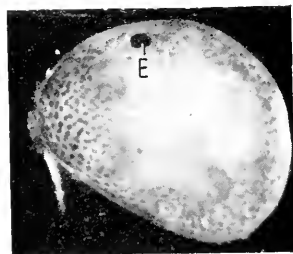


FIG. 205.

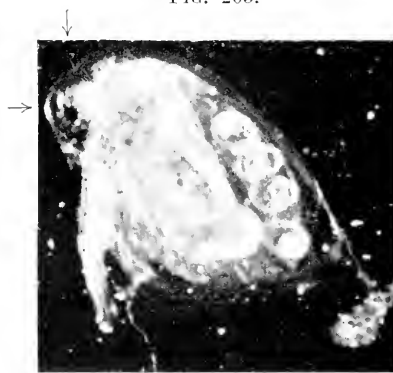


FIG. 206.

FIG. 204.—The dorsal surface of a Branchiopod, *Triops (Apus) cancriformis*. In the anterior region are two compound eyes, C, and behind them a median eye of the composite simple type, S.

FIG. 205.—An Ostracod, *Cyprina ophthalmica*. The single deeply pigmented eye, E, is seen shining through the semi-transparent shell.

FIG. 206.—The water-flea, *Daphnia*. Prominently in the head region (at the junction of the arrows) is the compound eye, appearing as a mass of pigment with little facets round it. Behind and underneath lies the minute composite median eye (see also Fig. 145).]

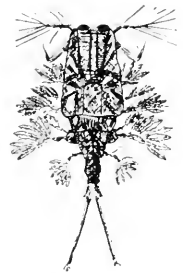
hermits the rocks between tidal marks in enormous numbers, and *Sacculina*, one of the most degenerate of parasites which becomes an endoparasite in the men of crabs.

The characteristic ocular feature of the whole group is the presence of a median unpaired eye; it is sometimes unique, as in *Cyclops*,

sometimes associated with a single compound eye, as in *Daphnia*, sometimes with paired lateral eyes which may be either simple, as in *Pontellopsis*, or compound in type, as in the Phyllopod, *Apus* (Fig. 204). In *Apus* the median eye is really a paired organ but the two are so closely situated that they appear on examination to be a single spot. The median eye of these small Crustaceans is situated either dorsal or ventral to the cervical ganglion and is of the composite simple type¹; it is composed of the fusion of a number of constituent ocelli (usually 3). Such a median eye is present in most of the Branchiopods and Ostracods, only occasionally degenerating when the compound eyes are particularly well developed (*Polyphemus*, *Leptodora*).

*Polyphemus*

The ocular arrangements in these actively swimming small Crustaceans is therefore very varied. The eyes of the water-flea, *Daphnia*, may be taken as representative of the Branchiopods and Ostracods. There is a single compound eye in the mid-line composed of 22 relatively rudimentary ommatidia (Fig. 206). Behind and below this, buried in the central nervous system, is the small composite ocellus (Figs. 131 and 145). It is interesting that the compound eye is actively motile, being kept in a state of continual vibration by 4 muscles somewhat resembling in their arrangement the rectus muscles of vertebrates (Rabl, 1901; Hess, 1912). It would seem that the small composite ocellus is of little functional value. The phototactic responses exhibited by the animal depend entirely upon the more elaborate compound eye; when this has been removed the phototactic responses fail although the more primitive generalized sensitivity to light persists (Schulz, 1928; Harris and Mason, 1956).

*Copilia*

The eyes of some of the actively swimming Copepods take on another form. In the female *Pontellopsis regalis*, there are two very small dorsal ocelli symmetrically placed and a large unpaired median eye situated fronto-ventrally underneath the rostrum; it has a large cuticular lens and 6 retinal cells arranged in an inverted position in two groups of 3, forming an intermediate step between a simple eye and an ommatidium (Vaissière, 1954-55). The elongated, actively motile eyes of *Copilia* are of the same general structure with a retinule of 3 sensory cells (Fig. 139) (Grenacher, 1880-95; Exner, 1891). This animal has two such eyes facing forwards and widely separated; in *Sapphirina* they are close together; and in *Corycaeus* so close that the lenses are fused in the mid-line.

*Balanus*

In sessile forms eyes are usually present in the actively swimming nauplius stage; thus in the acorn-shell, *Balanus*, there is initially a median unpaired eye but after several moults in the pupal stage two lateral composite eyes are acquired. In adult life, however, these become vestigial, as also does the unpaired eye of the ship-barnacle, *Lepas* (Fales, 1928). In some parasitic forms such as the fish-louse, *Caligus*, both median (simple) and lateral (composite) eyes are also present, but in degenerate types such as *Sacculina* eyes and other sense organs are lost.

*Lepas*¹ p. 152.

MYRIAPODA

The MYRIAPODS (the quick-moving, carnivorous solitary centipedes or Chilopoda, some with more, some with less than 100 legs, and the slow-moving vegetarian, gregarious millipedes or Diplopoda) are characterized by the possession of two groups of ocelli forming aggregate eyes on either side of the head so closely packed together as to suggest a compound eye (Figs. 207 to 210); so close are they in the Chilopod, *Scutigera*, that they form a pair of true compound eyes (Grenacher,

FIGS. 207 TO 210.—THE AGGREGATE EYES OF MYRIAPODS
(Specimens from Natural History Museum, London).

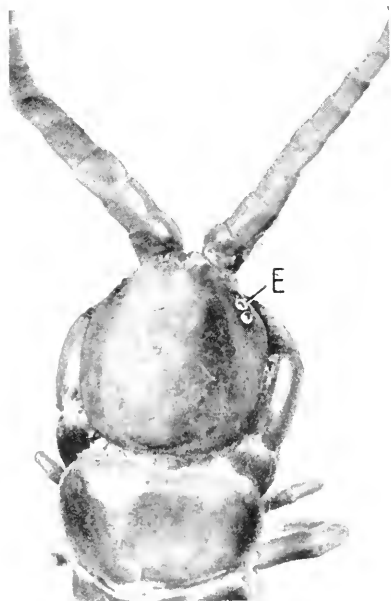


FIG. 207.

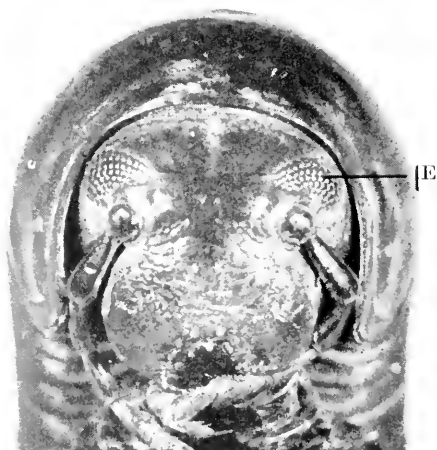


FIG. 208.

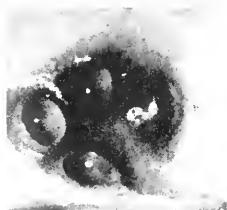


FIG. 209.



FIG. 210.

FIGS. 207 AND 209.—The centipede, *Scolopendra morsitans* from India. The group of 4 ocelli, E, are situated on either side of the head.
FIGS. 208 AND 210.—A Spirostreptid millipede from the Seychelles. The group of ocelli forming an aggregate eye, E, is seen on either side above the antennae. Fig. 210 shows the close resemblance to a true compound eye.

1880 ; Graber, 1880 ; Caesar, 1913 ; Constantineanu, 1930). In some types, such as *Pauropus*, which live in moist debris in the woods and forests, eyes are lacking.

ARACHNIDA

The ARACHNIDS form a large and loosely associated group which includes scorpions, king-crabs, spiders, pseudo-scorpions, whip-tailed scorpions, harvest-men, jerrymanders, mites and ticks. With the single exception of the king-crab they do not possess compound eyes

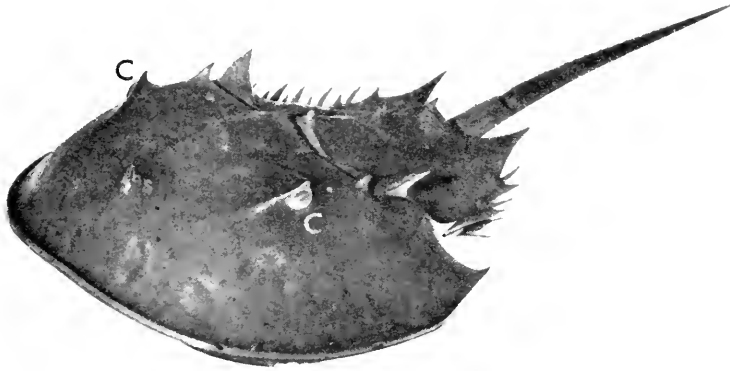
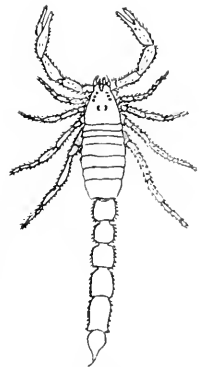


FIG. 211.—THE KING-CRAB, *LIMULUS POLYPHEMUS*.

A simple eye, S, is seen as a dark spot situated on either side of the median spine. The two compound eyes, C, are situated on the external aspect of each of the first lateral spines (specimen from Natural History Museum, London).

but all are provided with ocelli sometimes of considerable size and complexity.

SCORPIONS (SCORPIONIDEA), venomous animals up to 8 in. in length with a long stinging tail, are restricted to warm countries ; in habit they are essentially solitary and nocturnal, being active during the night and spending the day lurking under stones or in crevices. They are provided with a pair of large median eyes situated about the middle of the cephalothorax, and 2 to 6 pairs of lateral ocelli placed on its antero-lateral margins, the more anterior being simpler in structure than the posterior.¹ The lateral eyes are simple ocelli in which the



Scorpion

¹ p. 141.

borders of the visual cells unite with their neighbours to form rhabdomes (Fig. 109) ; the median eyes are also of the simple type with the sensory cells arranged in groups each centred on a rhabdome. These cells, however, are peculiar in that they are doubled upon themselves to form a semi-inverted retina ¹ (compare Fig. 127).²

The KING-CRABS (XIPHOSURA), a very ancient type dating to the Silurian, which live in shallow water on the sandy shores of North America (*Limulus*) or Asia, have two large lateral compound eyes and two median ocelli (Fig. 211). The compound eye is of a unique and elementary type ³ (Fig. 143) ; it is not faceted but is covered by a chitinous thickening of the cuticle which sends projections inwards as

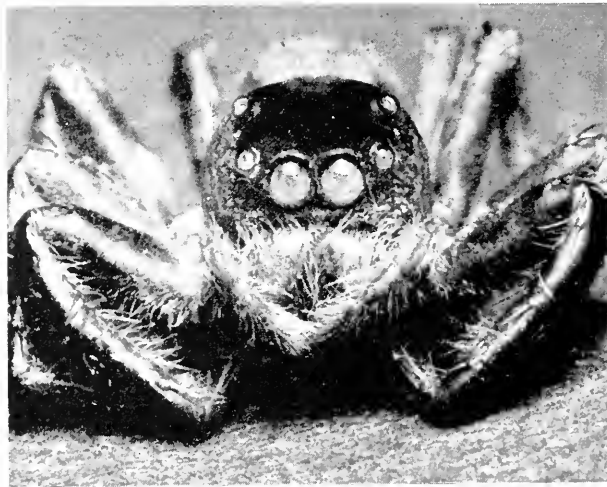


FIG. 212.—THE JUMPING SPIDER, *PLEXIPPUS SINUATUS*.

From the Dutch East Indies. The 2 large and 6 small simple eyes are seen surrounding the anterior and lateral aspects of the carapace (specimen from Natural History Museum, London).

conical papillae over each ommatidium to form a corneal lens. The small median eyes are of the simple type wherein the sensory cells are associated with rhabdomes (Fig. 142).

In addition, a third pair of ventral eyes is present in the larva on either side of the frontal organ of the hypostoma, an olfactory organ ; in the adult these eyes become degenerate but it is possible that they may participate in the olfactory function (Patten, 1893 ; Hanström, 1926).

¹ O.
² Details, see J. Müller (1826), Lankester and Bourne (1883), Parker (1887), Petrunkevich (1907), Police (1908), Scheuring (1913-14), Bütschli (1921), Versluys and De Meillon (1923).
³ p.

SPIDERS (ARANEIDA) are of widespread distribution and, although comprising some 14,000 species, are conveniently divided according to their habits into two types, the relatively sedentary "web-spinners" and the more active "wanderers" which hunt their prey: all, however, spin silk, either as a web, or for snaring or tying up their victims, for protection of their cocoons or for making bridges for travelling. In both types on the cephalothorax there are 6 or more usually 8 simple eyes arranged in two or three rows (Fig. 212); these have received a considerable amount of study.¹ The arrangement of these ocelli varies remarkably (Figs. 213 to 216). Among the web-spinners the ocelli are rudimentary and their effective range is short. The common house

FIGS. 213 TO 216.—THE ARRANGEMENT OF THE OCELLI IN DIFFERENT SPECIES OF SPIDERS.

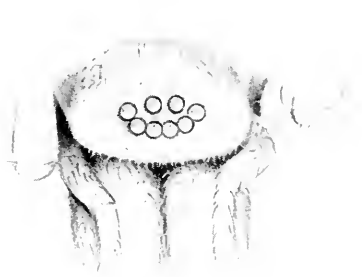


FIG. 213.—The ocelli of the common house spider, *Tegonuria domestica*.

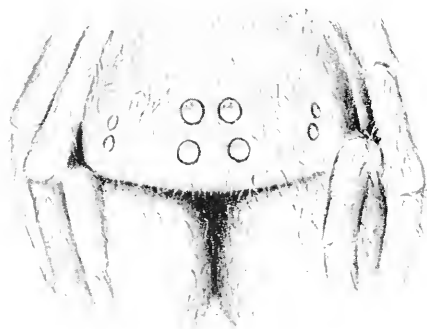


FIG. 214.—The ocelli of the common garden spider, *Araneus diadematus*.



FIG. 215.—The ocelli of the wolf spider, *Lycosa agricola*.

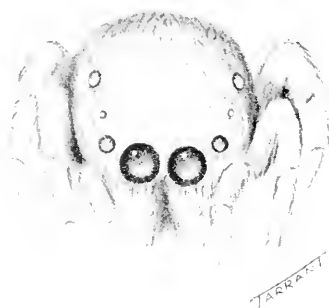


FIG. 216.—The ocelli of the jumping spider, *Salticus scenicus*.

¹ For details, see Hentschel (1899), Widmann (1908), Petrunkevitch (1911), Scheuring (1914), Versluys and Demoll (1923), Savory (1928), Homann (1928-53), Millot (1949).

*Tegenaria**Araneus**Lycosa**Salticus*

Whip-scorpion

spider, *Tegenaria domestica*, has two rows of 4 ocelli, those of the anterior row being slightly smaller than those of the posterior (Fig. 213); the common garden spider, *Araneus diadematus*, has 4 median and 4 small lateral eyes (Fig. 214). The more active hunting species which construct no web have larger eyes; thus the wolf-spider, *Lycosa*, has an anterior row of 4 small ocelli, two large posterior median and two smaller posterior lateral ocelli (Fig. 215); while the jumping-spider, *Salticus*, with a visual capacity more fully developed than the wolf-spider, has an anterior row of two large and two smaller ocelli on the front of its square-shaped cephalothorax, and two very small posterior median and two posterior lateral ocelli on the top (Fig. 216). With all its variations the general plan is thus consistent; the anterior median eyes (the two central eyes in the front row) have a verted retina, the remainder are inverted provided with a crystalline tapetum¹ and since these latter glow in the dark the former are sometimes called "diurnal eyes." The nerve-fibres from the two anterior median eyes travel—with a partial decussation at a chiasma—to the ganglion of the first cephalic segment, from the remaining eyes to that of the second (Figs. 107, 126).

It is interesting that the anterior median eyes of spiders are equipped with muscles attached to their posterior aspect rendering them motile so that they can increase their visual field; thus web-spiders have one muscle, Lycosids two, and Salticids six. These are absent in the lateral and posterior median eyes.

Curious anomalies to this general arrangement exist, but they are rare; thus in the female of a spider found in France, *Walckenaera acuminata*, the eyes are arranged on a dumpy tubercle on the cephalothorax, while in the male they are perched on a long stalk-like periscope, 4 on the tip and 4 half-way down (Millot, 1949). It is interesting that among spiders the lens, which is part of the outside covering of the animal, is cast at the time of moulting and thus it would appear that the spider may be rendered temporarily blind.

PSEUDO-SCORPIONS (PSEUDOSCORPIONIDEA), minute animals resembling miniature scorpions but without the long tail and sting, found burrowing in books or under stones, the bark of trees and the wing-covers of insects, are provided with two pairs of simple eyes (when they exist) on either side of the cephalothorax; these are typically equipped with an inverted retina and a tapetum (Scheuring, 1913) (Fig. 217).

WHIP-TAILED SCORPIONS (PEDIPALPI). The eyes of this order are not well known (Scheuring, 1913; Versluys and Demoll, 1923; Millot, 1949). They are entirely absent in some species; in others there are median eyes only; but the typical arrangement consists of two principal eyes and two groups of 3 lateral eyes.

Except *Salticus*, the eyes of which lack a tapetum and are therefore "diurnal". See p. 150.

The median eyes are of the cupulate type with a semi-inverted retina the cells of which are doubled upon themselves ¹ (Fig. 127). The lateral eyes have an inverted retina with a tapetum (Fig. 124).

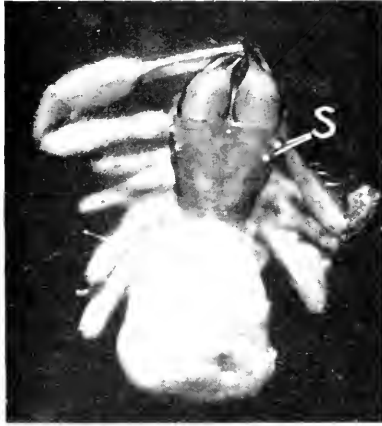


FIG. 217.—THE PSEUDOSCORPION, *CHTHONIUS ISCHNOCHULES*.

Showing two simple eyes, S, on either side (specimen from Natural History Museum).

HARVESTMEN (PHALANGIDA ; OPILIONES), minute spider-like Arachnids with extremely long legs, which avoid the glare of daylight, have two simple ocelli mounted one on either side of an oculiferous tubercle (ocularium) (Fig. 218). It would seem that with its laterally directed eyes the animal has no frontal vision. Each ocellus is a simple

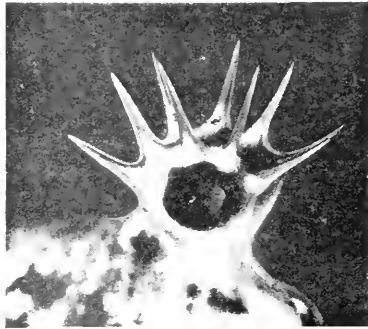
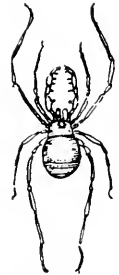


FIG. 218.—THE EYE OF THE HARVESTMAN, *MEGARHINUS DIADEMA*.

The simple eye is seen on a special oculiferous tubercle (specimen from Natural History Museum).



Harvestman

cupulate eye with a large cuticular lens and a simple row of visual cells from which the fibres emerge in several branches to form the optic nerve (Purcell, 1894).

¹ p. 150.



Jerrymander

JERRYMANDERS (SOLIFUGÆ)—active, pugnacious, non-venomous, nocturnal creatures found in warm countries—possess a pair of median (principal) eyes situated on a small tubercle and one or two pairs of lateral eyes usually rudimentary, difficult to see and probably functionless. Both types are simple cupulate ocelli with direct (verted) retinae (Scheuring, 1913; Demoll, 1917).

MITES and TICKS (ACARINA). MITES are minute Arachnids of which over 20,000 species are known, found almost universally in the earth or in water, salt and fresh, often of parasitic habit on or within animals

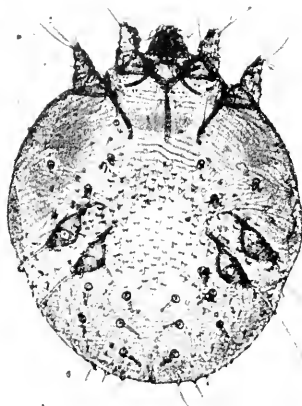


FIG. 219.—THE MITE, *SARCOPTES SCABIEI*.

(Female) ($\times 125$) (Sutton and Sutton, *Hb. of Dis. of the Skin*, Mosby).

(including man) and plants whether alive or decaying after death: well-known human parasites are *Sarcoptes scabiei* (the itch-mite) causing scabies, and *Demodex folliculorum* found in the hair follicles; the harvest-mite (chigger) is a virulent pest to both man and animals (particularly rodents), while others infest insects (Isle of Wight bee disease) and others plants (gall mites, red spiders, etc.). Many, such as *Sarcoptes* are without eyes (Fig. 219); others, such as the Prostigmata and the Hydracarina (fresh-water mites) are provided with 2, 4 or 6 ocelli on the front and lateral aspects of the head depending on the species, the individual organs being sometimes fused (Fig. 220 and 221) (Lang, 1905). Each possesses a convex lens often difficult to distinguish from the surrounding skin.

TICKS (IXODIDES) are larger than mites and are frequently of biological importance as causing disease (tick-fevers) in man¹ and animals.² Most types are without eyes, but such species may have thin transparent areas on the dorsal surface which perhaps respond to differences in the intensity of light. When visual organs are present they are extremely rudimentary, being minute ocelli mounted curiously on the animal's shoulder (Fig. 222).

FIGS. 220 AND 221.—THE EYES OF FRESH-WATER MITES (HYDRACARINA).



FIG. 220.—The 4 separate ocelli of *Limnesia*.



FIG. 221.—*Hygrobatas*, showing fusion of the anterior and posterior ocelli (after P. Lang).

¹ Texas fever, Rocky Mountain spotted fever, etc.

² Red-water fever in cattle, heart-water in sheep, etc.

SEA-SPIDERS (PYCNOGONIDA : PANTOPODA), marine species related to the Arachnids, inhabit the shores or the depths of the seas, living on seaweed, hydroids and sponges. They are provided with 4 primitive ocelli perched in two pairs on an oculiferous tubercle on the cephalothorax ; as we have already noted, the retinæ are of a peculiar and characteristic inverted type¹ (Morgan, 1891 ; Korschelt and Heider, 1893 ; Sokolow, 1911 ; Schlottke, 1933) (Fig. 125).



Pycnogonid

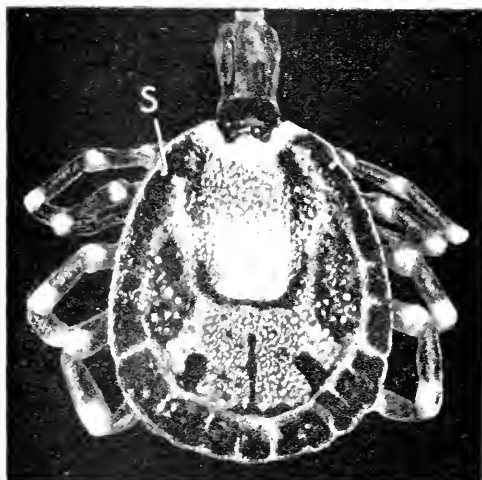


FIG. 222.—THE TICK, *AMBLYOMMA POMPOSUM*.

The two simple eyes, S, lie well posteriorly on the shoulder of the animal (specimen from Natural History Museum).

INSECTA

INSECTS form the largest class of Arthropods and their multitude of types is subdivided with reference to their possession of wings ; it is interesting that the complexity of their eyes varies directly with this characteristic, an association only natural in view of the demands made upon vision by a high degree of mobility.

(1) Sub-class APTERYGOTA (ἀ, privative ; πτέρυξ a wing), wingless forms, in which through a series of moults the adult differs little from the newly hatched insect except in size. They are the most primitive of insects, some species being marine, and when eyes are present they are simple in type.

THYSANURA—bristle-tails, of wide distribution in damp soil, some living between tide-marks or under stones or bark ; others (silver-fish) in bread-bins or books. Closely related are the eye-less DIPLURA.

PROTURA—minute creatures (2 mm.) living in moist soils under stones and bark, without wings, antennæ or eyes of any kind.

COLLEMBOLA—springtails, living under stones and leaves ; one species lives between tide-marks.

(2) Sub-class PTERYGOTA, provided with wings which, however, may be secondarily lost through highly evolved specialization. The sub-class is divided

¹ p. 150.

THE EYE IN EVOLUTION

TYPICAL INSECTS : I

(Drawn not to scale but approximately to a standard size.)

APTERYGOTA

THYSANURA



Silver-fish

PROTURA

*Acerentomon*

COLLEMBOLA



Springtail

EXOPTERYGOTA

ORTHOPTERA



Cockroach



Grasshopper



Stick-insect

DERMAPTERA



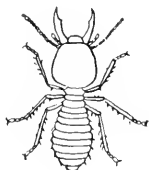
Earwig

PLECOPTERA



Stone-fly

ISOPTERA



Termite

PSOCOPTERA



Book-louse

ANOPLURA

*Pediculus*

EPHEMEROPTERA



fly

THYSANOPTERA



Thrip

HEMIPTERA



Bed-bug

TYPICAL INSECTS: II

(Drawn not to scale but approximately to a standard size.)

ENDOPTERYGOTA

NEUROPTERA



Lacewing

TRICHOPTERA



Caddis-fly

LEPIDOPTERA



Butterfly



Moth

COLEOPTERA

Colorado beetle,
LeptinotarsaBurying beetle,
NecrophorusRose-chafer,
CetoniaFire-fly,
Photinus

HYMENOPTERA

Bee, *Bombus*Wasp, *Vespa*

Ant

DIPTERA

Blue-bottle,
CalliphoraGad-fly,
TabanusBee-fly,
Bombylius

APHANIPTERA

Flea,
Pulex irritans

into two, depending on whether their wings are developed externally (Exopterygota) or internally (Endopterygota); in the latter the wings become evident only in the adult (imago) stage.

(a) EXOPTERYGOTA, insects which undergo a series of moults marked by the gradual development of wings. The more important orders are :—

ORTHOPTERA—cockroaches, locusts, grasshoppers, crickets, stick-insects, praying mantis.

DERMAPTERA—earwigs.

PLECOPTERA—stone-flies, a small and little known order, the aquatic larvæ being found beneath the stones of mountain streams, and the slow-flying adults having a very short life.

ISOPTERA—termites living under ground without eyes.

EMBIOPTERA—a few species of insignificant tropical insects.

ZORAPTERA—a few species of minute insects resembling termites.

PSOCOPTERA—small plump, book-lice (winged or wingless).

ANOPLURA—biting or sucking lice, wingless, parasitic on man and animals and frequently disease-producing (*Pediculus*, *Phthirus*, etc.).

EPHEMEROPTERA—mayflies, the aquatic larvæ living up to 3 years, the delicate adult a few hours.

ODONATA—brilliantly coloured dragonflies and demoiselle flies with aquatic larvæ, the former unusually active, swift-flying and voracious, the latter more delicate.

THYSANOPTERA—the minute thrips, vegetarian in habit, living on flowers, leaves and decayed vegetation.

HEMIPTERA—bugs with a specially developed proboscis (rostrum) adapted for piercing and sucking, many of them beautiful and slender despite their name : land bugs including the bed-bug, water bugs varying from the giant fish-killer or the water-scorpion to the water boatman (*Notonecta*), the cicadas, the frog-hoppers, tree-hoppers, leaf-hoppers, the aphids (or green-flies) and the scale-insects.

(b) ENDOPTERYGOTA, winged insects which have a complete metamorphosis (egg, larva, pupa, adult) with a resting pupa (or chrysalis).

NEUROPTERA—lace-wings, alder-flies, scorpion-flies.

TRICHOPTERA—caddis-flies, with aquatic larvæ and moth-like adults with hair-covered bodies and wings.

LEPIDOPTERA—butterflies and moths.

COLEOPTERA—beetles, including over 200,000 known species, both terrestrial and water-beetles.

STREPSIPTERA—*Stylops*, minute insects, parasitic on other insects, particularly wasps and bees.

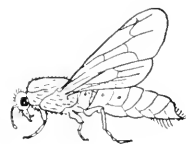
HYMENOPTERA—gall-flies, saw-flies, ichneumon-flies, bees, wasps, ants.

DIPTERA—two-winged flies, midges, gnats, mosquitoes and fruit-flies.

APHANIPTERA—the secondarily wingless fleas (jiggers, etc.), blood-sucking in habit and parasitic on birds and mammals.

In the larval form all insects possess simple lateral eyes (STEMMATA; στεμματα, a garland). The adult also frequently possesses simple eyes (DOE OCELLI), although they are absent or vestigial in many species, as in most beetles and mosquitoes, some families of flies, and noctuid moths. But in addition it is provided with MULTIFACETED COMPOUND EYES. In this generalization there are some exceptions in degenerative

forms which are unprovided with compound eyes—the primitive wingless Collembola (Fig. 223), lice and parasitic fleas which possess only ocelli (Fig. 224), while species which live in darkness may be unprovided with eyes, such as the Protura, the driver ant of Africa, *Dorylus* (with the exception of the winged male), or most termites. The winged male *Stylops* has aggregate eyes composed of a multitude of ocelli so closely packed together as to resemble a compound eye, but the parasitic female which passes its whole life within its host, is unprovided with eyes.¹



Male driver ant

FIGS. 223 AND 224.—INSECTS WITH OCELLI AND NO COMPOUND EYES
(Natural History Museum, London).



FIG. 223.—The springtail, *Archistoma besselsi* (Collembola).

There are 8 ocelli on each side and no compound eyes.



FIG. 224.—The bird-louse, *Trintodon aculeatum* (Anoplura).

There are 2 simple eyes (S) on each side and no compound eyes.

We shall see² that the compound eyes are the dominant organs in the adult insect, the simple eyes essentially accessory; this is seen in the occasional disappearance of the latter as the former develop. Thus the larva of the water-beetle, *Dytiscus*, has 6 ocelli on each side of the head, but in the later stages of larval development the compound eye appears in front of them, first as a crescentic area on each side. At the stage of moulting the cornea of the ocelli are shed with the cuticle and as the compound eye rapidly develops the bodies of the ocelli recede, remaining, however, permanently attached in vestigial form to the optic nerves.

¹ For the descriptive anatomy of the compound eyes of Insects, see p. 166; for that of the ocelli, see Hesse (1901), Merton (1905), Link (1908-9), Strohm (1910), Demoll and Scheuring (1912), Bugnion and Popoff (1914), Melin (1923), Homann (1924), Hamilton (1925), Zikan (1929), Wolsky (1930-31), Friederichs (1931), Verrier (1940), Lhoste (1941).

² p. 224.



Female driver ant

*Stylops*

FIGS. 225 TO 227.—THE COMPOUND EYES OF INSECTS.

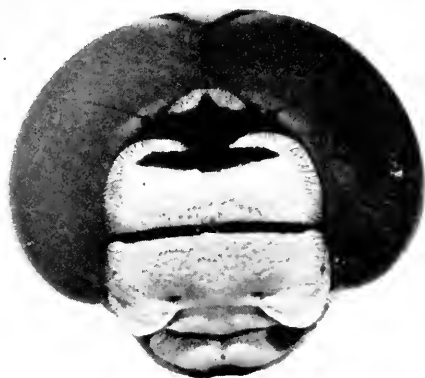


FIG. 225.—The head of the dragon-fly, *Eschna californica* (Odonata) capped by two enormous crescent-like compound eyes (James Needham).



FIG. 226.—The male gadfly, *Ancala fasciata nilotica* (Diptera).

The immense compound eyes occupy the whole of the surface of the head (Natural History Museum, London).



FIG. 227.—The cave-bug, *Leotichius glaucopsis* (Hemiptera).

From Malaya. Dorsal surface. The 2 prominent compound eyes (C) are largely spread over the ventral surface. There are 2 median ocelli (S) (Natural History Museum, London).

THE STEMMATA (OR LATERAL OCELLI) OF LARVAL OR PUPAL FORMS can in general be classified into two main types. The most elaborate organs are seen in the larvæ of Lepidoptera and Trichoptera; these are arranged in a group of variable size¹ on either side of the head, each separate individual of which takes the form of the single ommatidium of a compound eye with a cuticular corneal lens,

g., 6 on either side of the head in the caterpillars of butterflies.

FIGS. 228 AND 229.—STALKED COMPOUND EYES.

FIG. 228.—A grouse locust, *Ophiottettix limosina* (Orthoptera).

The compound eyes (C) are placed on either side at the end of the stalk-like head. (One antenna is missing.) (Natural History Museum, London.)

FIG. 229.—The stalk-eyed fly, *Achias rothschildi* (Diptera).

The large compound eyes (C) are at the end of unusually long stalks (Natural History Museum, London).

a crystalline cone and a retinule of 7 sensory cells grouped around a rhabdome (Fig. 138) (Dethier, 1942-43). A more simple variety is seen in the larvæ of Tenthredinidæ (saw-flies) and Coleoptera. These usually have two lateral eyes of cupulate shape with a retina formed as a palisade of sensory cells under a lens-like thickening of the cuticle. The reticular cells are arranged in groups of two or three, each group around an elementary rhabdome which is not constructed for the reception of images. More rudimentary forms occur such as the



Sawfly

simple pair of visual cells with two overlying pigment cells which form the eye of the larva of the midge, *Ceratopogon*, or the few light-sensitive cells lying in a shaded pocket in the pharyngeal skeleton of the larva of the house-fly, *Musca* (Fig. 99) (Welsh, 1937 ; Debaisieux, 1939).

THE DORSAL OCELLI OF ADULTS were described and figured as early as 1678 by the French scientist, de la Hire (Figs. 149, 227, 230). They are usually three in number arranged in triangular form, one median and anterior and two lateral and posterior on the dorsal aspect of the

FIGS. 230 AND 231.—UNUSUAL COMPOUND EYES IN INSECTS (Natural History Museum, London).

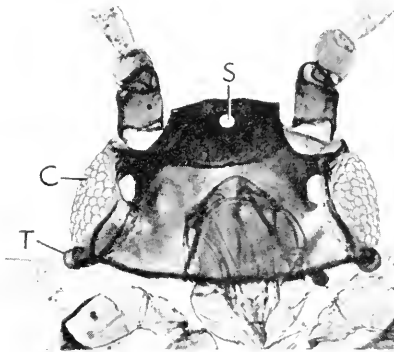


FIG. 230.—The aphid, *Dactynotus obscurus* (Homoptera).

There are 2 compound eyes (C) one on each side of the head, and, in winged forms, 3 ocelli on the vertex of the head, the median one of which is marked S. In the family Aphididae there is in addition a prominence, the triommatidium (T), of unknown function, bearing 3 facets at the base of each compound eye. This organ is always present, even in those forms in which a compound eye is lacking.

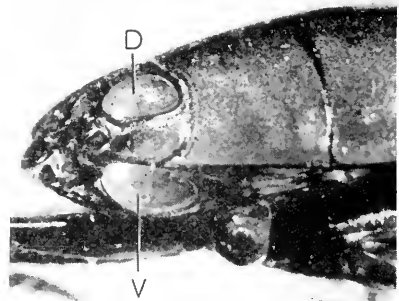


FIG. 231.—The Whirligig beetle, *Dineutus grossus* (Coleoptera).

There are 2 compound eyes on each side of the head, one dorsal (D) for aerial vision, and one ventral (V) for vision under water.

head between the compound eyes ; but they are small and inconspicuous, being often hidden by scales as in moths or hairs as in bees. In some species of ants belonging to the sub-family Myrmicinae, the anterior ocelli are double or binary in type (Weber, 1947). In others, such as Orthoptera, the ocelli are vestigial ; in general, their degree of development shows some correlation with that of the wings (Kalmus, 1945). As a rule they resemble in structure the more simple type of stenopæa, being comprised merely of a group of visual cells associated with ommatidia lying beneath a common euticular lens (Fig. 108).

THE COMPOUND EYES OF ADULTS are laterally situated on the head and form the essential visual organ (Fig. 149). They are large and

prominent and vary in complexity from the small organ of the worker of the ant, *Solenopsis*, which lives underground and is provided with 6 or 8 facets, to the elaborate organ of dragon-flies (Odonata) with up to 28,000¹ ommatidia (Imms, 1935) (Figs 225 to 227). Occasionally the compound eyes are enormous, literally occupying the whole surface of the head, as is seen in the gad-flies (Tabanidae) (Fig. 226); usually they are situated on the surface of the head, sometimes they stand out prominently as in the praying mantis (Fig. 734), but occasionally they are perched on long stalks (Figs. 228 and 229). Exceptionally two compound eyes are differentiated in function, such as in the whirligig beetle, *Dineutus*, which has a dorsal compound eye for aerial vision and a ventral for vision under water (Fig. 231).² A unique organ is seen in the Aphid family ("green-fly") in which an additional tri-faceted organ, the TRIOMMATIDION, is found at the base of each compound eye (Fig. 230); the function of this organ is unknown but it is present even in those forms of aphids which have no compound eyes.



Dragon-fly



Whirligig beetle



Aphid

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¹ p. 172.² Compare the eye of *Anableps*, p. 324.

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CHAPTER VIII

THE EYES OF PROTO-CHORDATES

THE Chordates constitute a phylum characterized by a dorsal tubular nerve-cord, a dorsal supporting axis (a notochord) and pharyngeal gill-slits ; the last two, however, may be temporary in duration. The Vertebrates constitute a sub-phylum within the Chordates which possesses as distinctive characters a head and skull, a brain with eyes, a vertebral column, and (generally) paired limbs. Stumbling on the



FIG. 232.—*BALANOGLOSSUS*.

The long tongue-like proboscis (Pr) resembles an acorn ($\beta\alpha\lambda\alpha\nu\omicron\varsigma$, an acorn ; $\gamma\lambda\omega\sigma\sigma\alpha$, a tongue).

border-line between Invertebrates and Vertebrates are three classes of animals (Proto-chordates) possessed of a rudimentary nerve-cord, a notochord and gill-clefts—the Hemichordates, the Tunicates, and the Lancelets. Apart from the pelagic Tunicates, these lowly creatures are either sessile or burrowing in habit.

The HEMICHORDATA are typified in *Balanoglossus*, a worm-like marine creature burrowing in the sand and mud of most seas (Fig. 232).

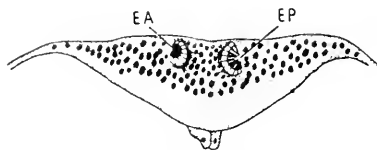


FIG. 233.—THE EYES IN THE TORNARIA LARVA OF *BALANOGLOSSUS*.

Antero-posterior section through the apical plate showing the anterior, EA, and posterior, EP, eyes (after Morgan).

The nervous system arises as a longitudinal groove of ectoderm which becomes tubular but gives no evidence of visual out-pouchings. In the larvæ (tornaria) of some species situated on the apical plate there are two eye-spots consisting of cup-shaped depressions of clear cells surrounded by pigment (Fig. 233), but in the adult there are no special sense organs (Spengel, 1893 ; Stiasny, 1914).



FIG. 234.—THE SEA-SQUIRT, *Ascidia*.

The adult covered by its tunic (*test*), the lower end attached to a rock, the upper end ending in an inhalant siphon (mouth), and on the morphological dorsal surface an exhalant siphon (atrial opening). Around both apertures there are sometimes pigment spots of unknown character. During life, the animal draws water in through the first and expels it from the second; if irritated, water is forcibly expelled from both, hence the name "sea-squirt."

mentary cellular lens. It is interesting that the visual cells are morphologically inverted inasmuch as they face towards the cavity of the sensory vesicle while the intrinsic lens faces towards the brain as if it would be effective only for light traversing the transparent body of the animal.

In free-swimming Tunicates visual organs may persist; thus in the asexual form of *Salpa* there is a single median horse-shoe-shaped ocellus and sometimes smaller accessory ocelli on the dorsal aspect of the animal closely associated with the single nerve ganglion.

The LANCELETS (ACRANIA; CEPHALOCHORDATA) are variously regarded as a pioneer offshoot from the chordate stock or as a degenerate member of the phylum. They possess a dorsal tubular nerve-cord, a notochord and a tail, but lack a differentiated brain or eyes. They are typified in the common lancelet,

The TUNICATA (UROCHORDATA) are typified in the Ascidians or sea-squirts (Fig. 234). *Ascidia* in its free-swimming larval stage is a tadpole-like creature, about 1.0 mm. in length, possessing the chordate characteristics of a brain and a dorsal tubular nervous system, a notochord and gill-slits. At this stage it is provided with a single cerebral eye associated with a statocyst, but as the hermaphroditic adult settles to its sedentary plant-like life within its thick tunic of cellulose and attaches itself to rocks or weeds, the nervous system is reduced to a single ganglion above the pharynx and the eye disappears. In some of these forms the siphons respond to light by retraction. It is true that pigmented spots are found around the siphonal openings, which used to be considered "ocelli", but in *Ciona*, at any rate, they are in fact not light-sensitive (Millott, 1957).

The transient eye of the larval Ascidian is of unusual interest (Kowalevsky, 1871; von Kupffer, 1872; Froriep, 1906). It arises as an out-pouching of the cerebral vesicle which forms a single sensory organ consisting of a sac containing a statocyst and an extremely elementary eye on its dorso-posterior wall (Fig. 235). The retina is composed of a few sensory cells derived from the inner wall of the neural tube; it is capped with pigment and above it lies a rudimentary

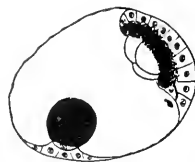


FIG. 235.—THE EYE OF THE ASCIDIAN TADPOLE

Diagram of the sensory vesicle with a unicellular otolith and an ocellus (above right) with retinal cells, pigment and 3 lens cells situated towards the cavity of the vesicle (Berrill, *The Origin of Vertebrates*, Oxon., 1955).

Branchiostoma (Amphioxus) lanceolatum, a small translucent fish-like marine creature about 2 in. in length the body of which is divided into 62 myotomes (Fig. 236). Although possessing no definitive eyes, the animal is strongly photo-negative and sensory organs occur, some possibly in the surface ectoderm and others deeply placed in relation to the neural tube which tend to enforce upon the animal its burrowing habit.

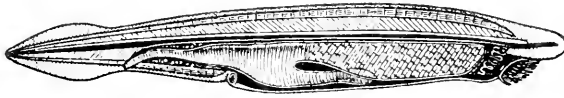


FIG. 236.—THE LANCELET, *AMPHIOXUS*.

The head end is towards the right, the tail end to the left (after Haeckel).

The superficial sensory organs are the large isolated CELLS OF JOSEPH (1904–28), associated with the surface epithelium on the dorsal aspect, which were claimed by this investigator to be light-sensitive (Fig. 237); this view, however, is by no means substantiated.

The neural photosensitive organs are of two types (Fig. 237). Towards the cephalic end of the animal a small median area of ependymal cells lining the central canal of the nerve-cord is specially differentiated to form an INFUNDIBULAR ORGAN which appears to be light-sensitive and is functionally allied to a

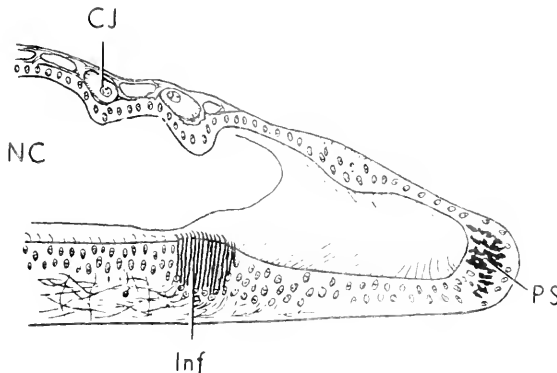


FIG. 237.—SAGITTAL SECTION OF THE ANTERIOR PORTION OF *AMPHIOXUS*.

CJ, cells of Joseph ; Inf, infundibulum ; NC, neural canal ; PS, anterior pigment spot (after Boeke).

dark pigment-spot situated at the head end of the animal. The pigment-spot was originally described as an "eye-spot" by Johannes Müller in 1842, and used to be credited with light-sensitive properties and specific connections with the central nervous system¹; it was indeed held to be the phylogenetic precursor of the vertebrate eye. Its specific innervation, however, was contested initially by Kohl (1890) and conclusively by Franz (1923), and a visual function excluded

¹ See the writings of W. Müller (1874), Langerhans (1876), Ayers (1890), Joseph (1904–28), Edinger (1906), Boeke (1908), Pietschmann (1929).

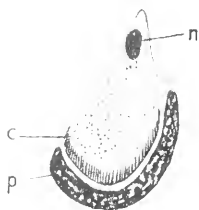


FIG. 238.—VISUAL CELL OF *AMPHIOXUS*.

n, nucleus; c, striated margin; p, pigment mantle.

by the experiments of Nagel (1896) and Hesse (1898) and more particularly by those of Parker (1908) and Crozier (1917). There would seem little doubt that it is not a vestigial eye but that its function is to endow the infundibular organ with directional ability by casting a shadow upon it when the animal or the light source moves, a primitive role we have already seen in the eye-spot of the Protozoon, *Euglena*¹ (Franz, 1912-34; Wollenhaupt, 1934).

A second photosensitive mechanism is seen in the ORGANS OF HESSE (1898), individual cells scattered on the ventral and lateral aspects of the nerve-cord towards its posterior end (Figs. 238 and 239). These are single large ganglion cells variously orientated, each provided with a brush-like ciliated margin and an issuing nerve-fibre, each capped by a crescent-shaped pigment cell to give it directional ability. The distribution and structure of these unique cells have been fully studied by a number of observers (Franz, 1923; Joseph, 1928; Kohner, 1928; Wollenhaupt, 1934) and their photosensory function established by Parker (1908) and Crozier (1917).

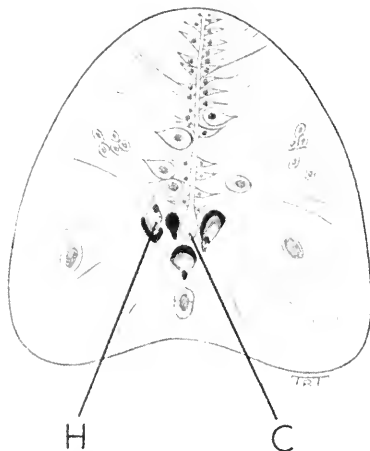


FIG. 239.—THE NEURAL VISUAL CELLS OF *AMPHIOXUS*.

Section through the spinal cord in the region of the 5th segment, showing the central canal, C, and the large visual cells of Hesse, H, with their associated pigment cells (after Hesse).

Ayers. *Zool. Anz.*, **13**, 504 (1890).

Bock. *Anat. Anz.*, **32**, 473 (1908).

Crozier. *Anat. Rec.*, **11**, 520 (1917).

Edwards. *Anat. Anz.*, **28**, 417 (1906).

Franz. *Zool. Zbl.*, **32**, 375 (1912).

Joseph. *Arch. Anz.*, **59**, 401 (1923).

Kohner. *vergl. Anat. d. Wirbeltiere*,

1, 989 (1934).

Froriep. *Handbuch d. vergl. und exper. Entwicklungslehre d. Wirbeltiere*, Jena, **2** (1906).

Anat. Anz. (suppl.), **29**, 145 (1906).

Hesse, R. *Z. wiss. Zool.*, **63**, 456 (1898).

Joseph. *Anat. Anz.* (suppl.), **25**, 16 (1904).

Biol. generalis, **4**, 237 (1928).

Kohl. *Zool. Anz.*, **13**, 182 (1890).

¹ p. 126.

- Kolmer. *Biol. generalis*, **4**, 256 (1928).
 Kowalevsky. *Arch. mikr. Anat.*, **7**, 101 (1871).
 von Kupffer. *Arch. mikr. Anat.*, **8**, 358 (1872).
 Langerhans. *Arch. mikr. Anat.*, **12**, 290 (1876).
 Millott. *Endeavour*, **16**, 19 (1957).
 Müller, J. *Abh. Kgl. Akad. Wiss.*, Berlin (1842).
 Müller, W. *Ü. d. Stammesentwicklung d. Sehorgans d. Wirbelthiere*, Leipzig (1874).
 Nagel. *Der Lichtsinn augenloser Tiere : eine biologische Studie*, Jena (1896).
 Parker. *Proc. Amer. Acad. Arts Sci.*, **43**, 415 (1908).
Amer. Nat., **42**, 601 (1908).
 Pietschmann. *Kükenthal's Handbuch der Zoologie*, Berlin (1929).
 Spengel. *Fauna e Flora Golf. Napoli*, **18**, 1 (1893).
 Stiasny. *Z. wiss. Zool.*, **110**, 36 (1914).
 Wollenhaupt. *Jena. Z. Naturw.*, **69**, 193 (1934).



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

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.

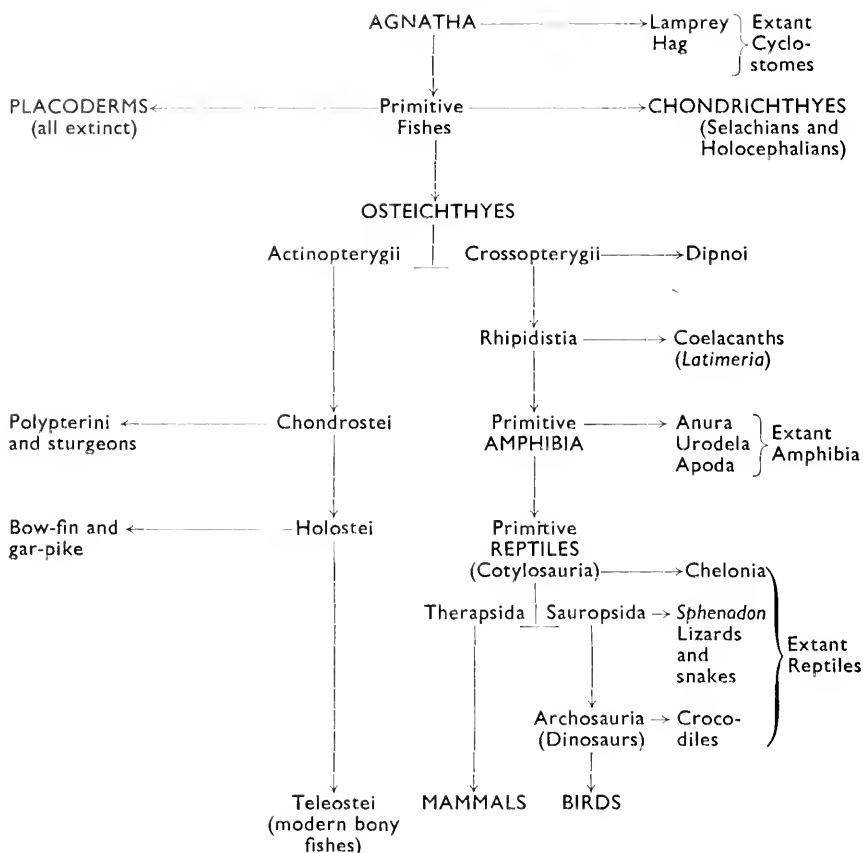
The VERTEBRATE PHYLUM is of enormous antiquity and stems from the primitive Agnatha, jaw-less pre-fishes, the fossil remnants of which are 400 million years old and are found abundantly in ancient Silurian rocks. Their ancestors are unknown¹ but their descendants have become the lords of the earth. It 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

¹ 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).

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



Pr. Am.



Primitive Reptile

Dinosaur, *Diplodocus*

Therapsidan

Cyclostomes, the lamprey and the hag. From these there evolved somewhere in the Upper Silurian period, 350 million years ago,¹ 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 *Colacanth*, *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 *Cecilians* (*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

¹ 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 an anatomical point of view—and certainly from the aspect of the structure of the eye—these six classes of the Vertebrates, neglecting the Cyclostomes, may 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.¹

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

¹ 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.¹ 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 era²—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 ammocete (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”.³ 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 is evident to Aristotle and was firmly drawn by Lamarck in 1809. The pedigree of the former—presumably from the latter—still remains unknown and all the theories which have been advanced

¹ p.² 320 to 350 million years ago, p. 754.³ 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,¹ 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,² 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* (*forecole optica*). 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

¹ 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.

² p. 532.

THE EYE IN EVOLUTION

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

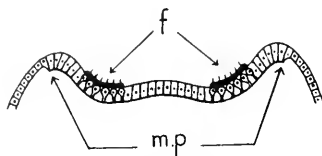


FIG. 242.

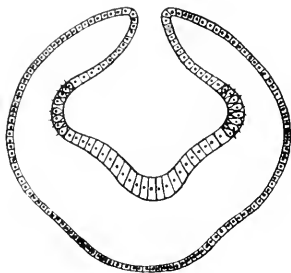


FIG. 243.



FIG. 244.

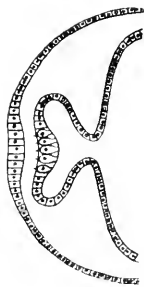


FIG. 245.

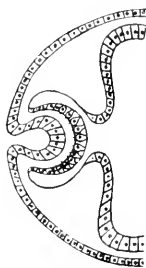


FIG. 246.

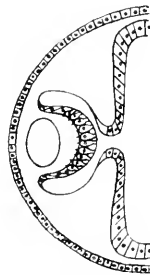


FIG. 247.

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 neurofibrils 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,¹ 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.² 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.

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

¹ p. 146.

² 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 involuted 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,¹ 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.²

¹ See, for example, Balfour (1881), Dohrn (1885), Keibel (1906), Froriep (1906), Lange (1908), Franz (1910) and others.

² 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.

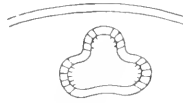


FIG. 252.



FIG. 249.

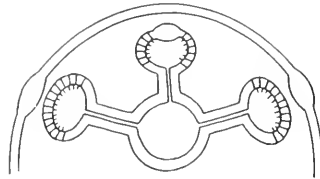


FIG. 253.

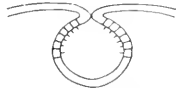


FIG. 250.

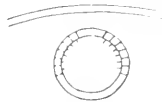


FIG. 251.

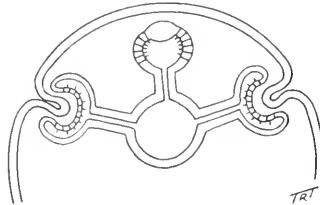


FIG. 254.

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*¹; 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.

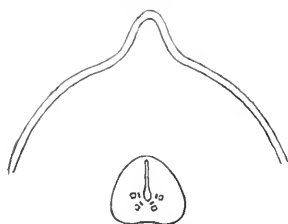


FIG. 255.—Symmetrical arrangement of the organs of Hesse with pigment cells facing the central canal.

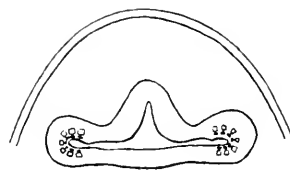


FIG. 256.—Evagination of the canal carrying with it the organs of Hesse.

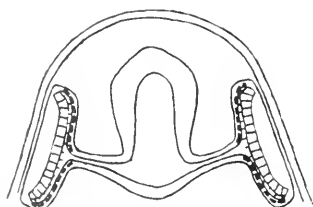


FIG. 257.—Invagination to form a sensory and pigmented layer.

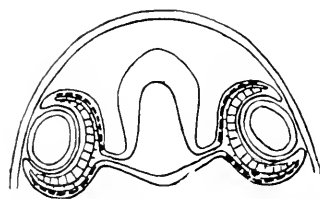


FIG. 258.—Secondary invagination of the lens vesicle (from Walls, after Boveri).

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 Vertebrates² (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 Schwann, believe that they are endoneural. Thus Boveri (1904) traced their origin from the ganglion-like cells of Hesse in an *Amphioxus*-like ancestor. In this view he was supported by Parker (1908-9),

¹ p. 229.

² p. 537.

³ 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.

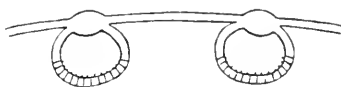


FIG. 259.

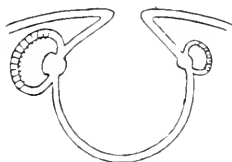


FIG. 260.

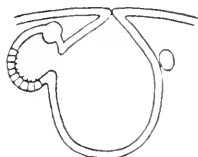


FIG. 261.

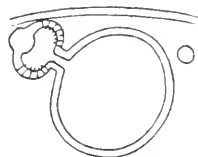


FIG. 262.

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 tadpole¹ 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

¹ 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 obvious¹; 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, that a lens will form from undifferentiated ectoderm at an abnormal site if the optic cup is transplanted thereto. Others have

¹ See, for example, 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.¹ 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.

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

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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 forms¹) 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.
NEURONE II (conductive and associative elements)	{ 4. Inner nuclear layer (bipolar, horizontal and amacrine cells).
	{ 5. Inner plexiform layer.
NEURONE III (conductive elements)	{ 6. Ganglion cell layer.
	{ 7. Nerve fibre layer.

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

¹ 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

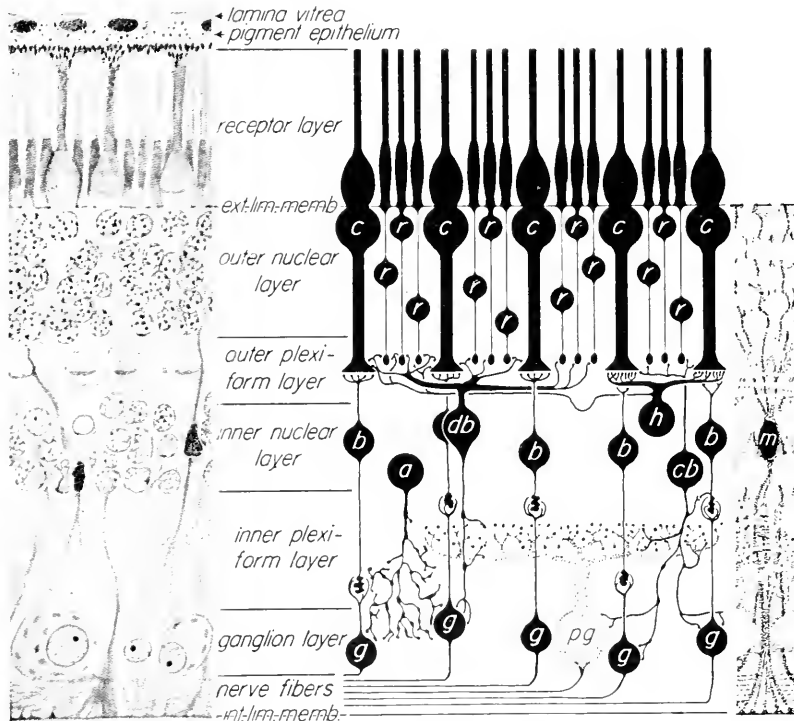


FIG. 263.—THE HUMAN RETINA.

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.¹ 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

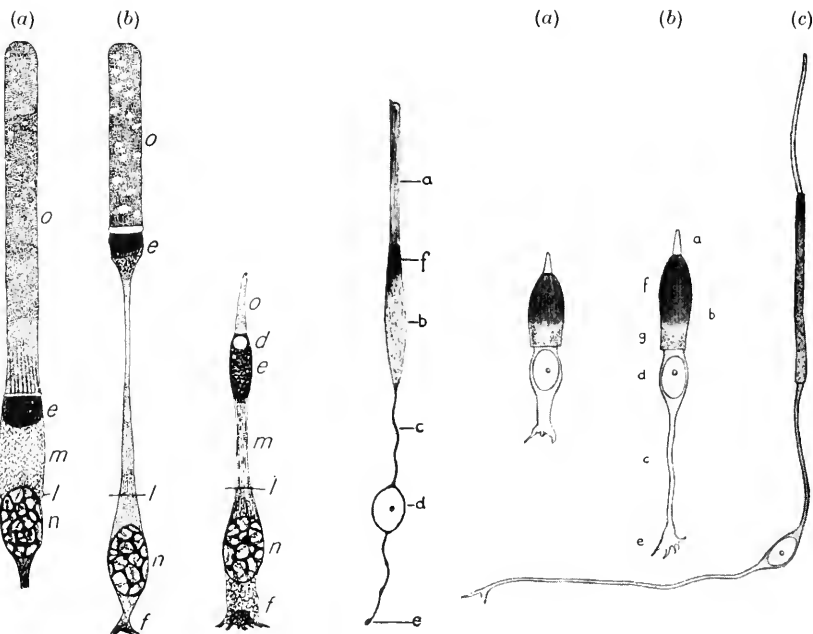


FIG. 264.

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

¹ 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 fractometry).

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: Greeff, 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 A₁ (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 retene₁ as a chromophore and produce a pigment with an absorpt. 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.¹ 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* (Lyll, 1956).²

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

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

² 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

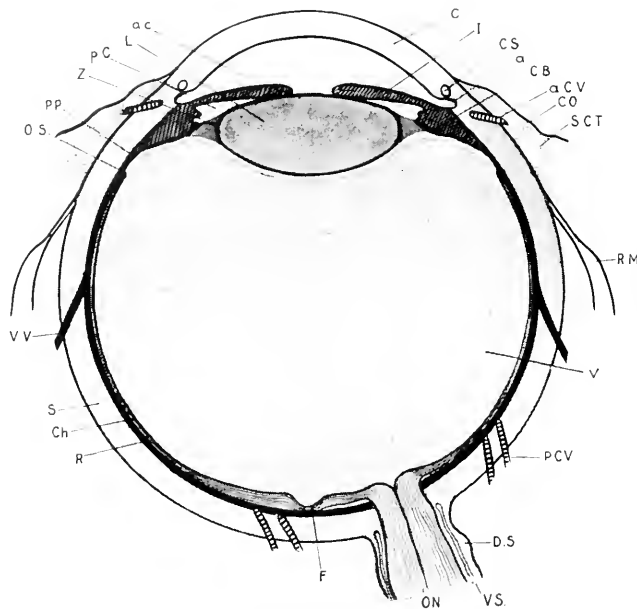


FIG. 268.—DIAGRAM OF THE LONGITUDINAL SECTION OF THE HUMAN EYEBALL.

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 stenopœic 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.

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FIG. 269.—D. W. SOEMMERRING (1793-1871).

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 Zinn² and Young,³ while compendia had been published by such authors as Blumenbach,⁴ Albers,⁵ and Cuvier⁶; 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 cysticereus in the human eye (1830).

The CYCLOSTOMES (κύκλος, round; στόμαχ, 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 stage⁷; 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.

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 lamprey (*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 lampreys (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 *Ammocetes* (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 develops¹; 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 ammocetes 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 AMMOCCETE EYE

Since the original description by W. Müller (1875), several studies have been made of the ammocete 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

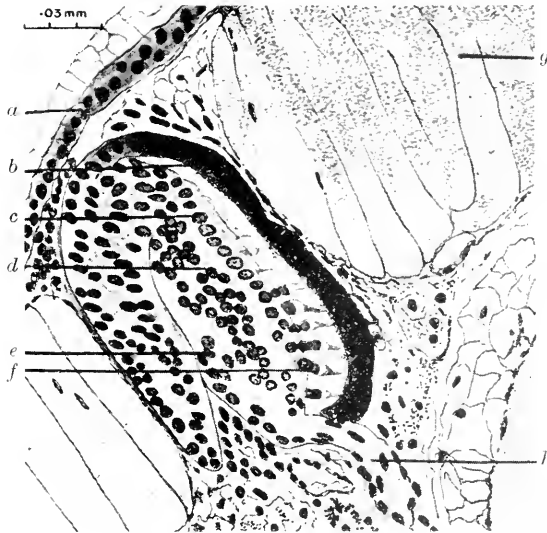


FIG. 271.—SECTION THROUGH THE EYE OF THE AMMOCCETES (THE LARVA OF *PETROMYZON FLUVIATILIS*).

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

THE EYE IN EVOLUTION

FIGS. 272 AND 273.—THE AMMOCETE EYE (after Stúdnicka).

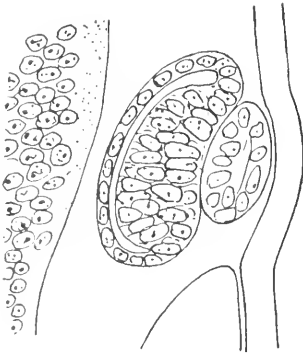


FIG. 272. —The eye of the 8 mm. larva of *Petromyzon*, showing the optic vesicle and the smaller lens vesicle superficial to it.

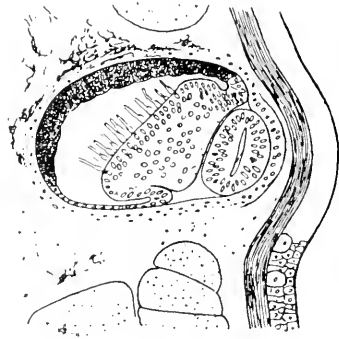


FIG. 273. —The eye of the 18 mm. ammocetes showing the lens vesicle incorporated into the optic vesicle. In the latter the outer pigmented layer and the highly differentiated inner layer with the projecting visual cells are evident.

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

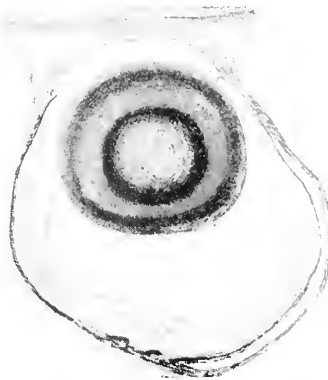


FIG. 274. —THE EYE OF THE AMMOCETES.

a late stage. On top is the surface epithelium, underneath which lies the mesodermal skin. Underneath this is the scleral cornea. The lens is fully formed, as also are the anterior and vitreous chambers (a drawing from Mawas).

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 myxinoïd, *Bellostoma*, 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 ammocetes there are numerous interesting cells copiously innervated from the lateral line. Morphologically they resemble the apolar visual cells seen in the earthworm or

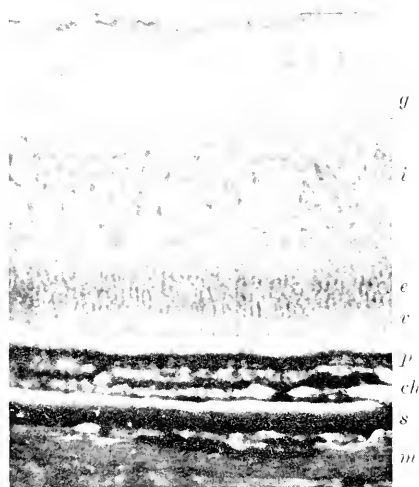


FIG. 275. SECTION THROUGH THE POSTERIOR SEGMENT OF THE EYE OF THE FULLY DEVELOPED AMMOCETES.

g, ganglion cells ; *i*, internal nuclear layer ; *e*, external nuclear layer ; *r*, visual cells ; *p*, pigmented epithelium ; *ch*, choroid ; *s*, sclera ; *m*, muscular tissue (Azan, $\times 250$) (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 Joseph¹ ; 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.

THE EYE IN EVOLUTION

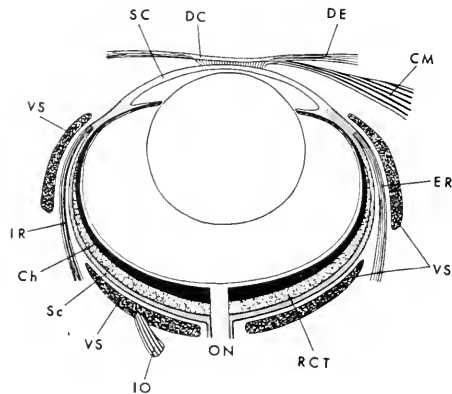
FIGS. 276 AND 277.—THE EYE OF *LAMPETRA PLANERI*.

FIG. 276.

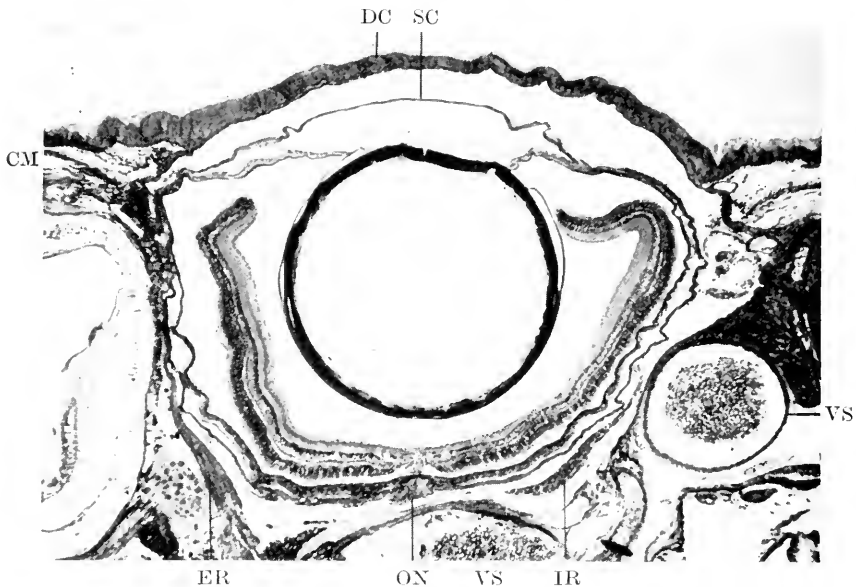


FIG. 277.

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 ($\times 34$) (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, sclera ; 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 endymal 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.”

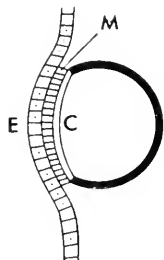


FIG. 278.—The primary spectacle of Cyclostomes and aquatic Amphibians.

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

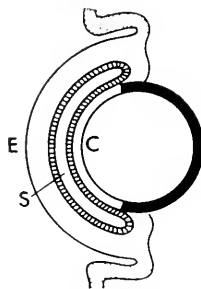


FIG. 279.—The secondary spectacle as seen particularly in Reptiles.

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 choroideae of Teleosts; 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. r. 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,

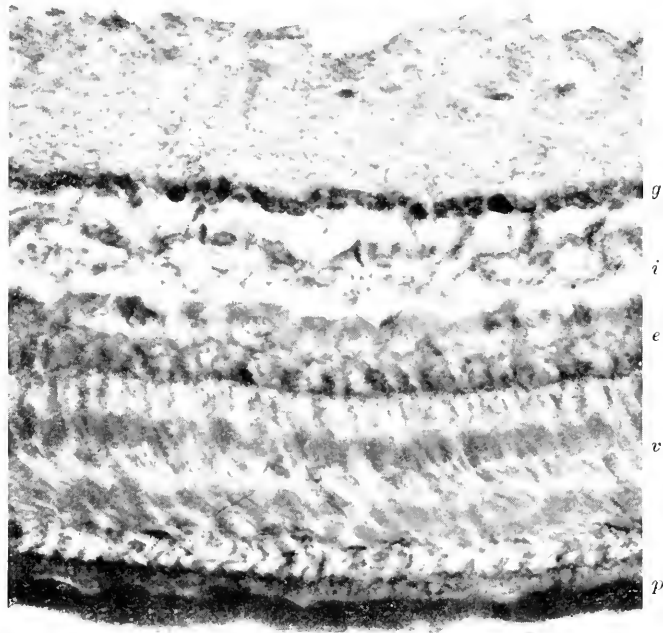


FIG. 280.—THE RETINA OF *LAMPETRA FLUVIATILIS*.

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, $\times 370$) (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

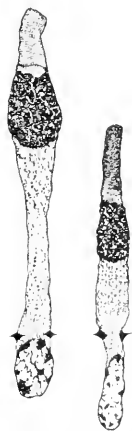


FIG. 281.—THE VISUAL CELLS OF THE ATLANTIC LAMPREY, *PETROMYZON MARINUS*.

Showing the "long" and the "short" elements ($\times 1,000$) (Gordon Walls).

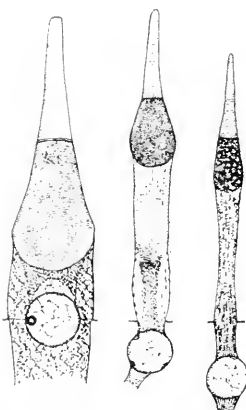


FIG. 282.—THE VISUAL CELLS OF THE NEW ZEALAND LAMPREY, *GEOTRIA AUSTRALIS*.

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 ($\times 1,000$) (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.

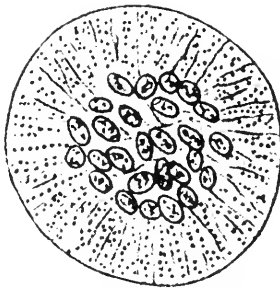


FIG. 283.—The optic nerve of the ammocete larva (after Stúdnicka).

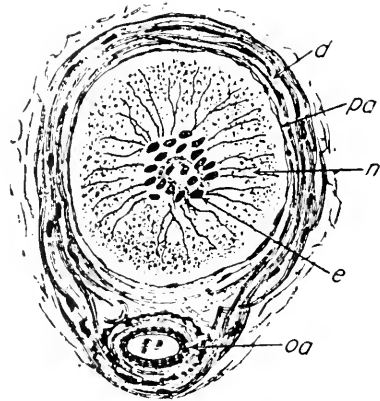


FIG. 284.—The optic nerve of *Lampetra fluviatilis* (after Dückler).

In both cases there is no septal system but merely an axial column of endodermal 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*, endodermal cells sending out radiating processes; *oa*, ophthalmic artery.

of cell-bodies, probably endodermal 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 dioptries) 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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¹ p. 644.

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CHAPTER XI

THE EYES OF FISHES

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

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

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

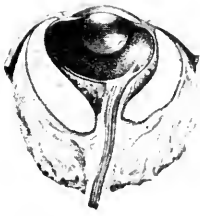
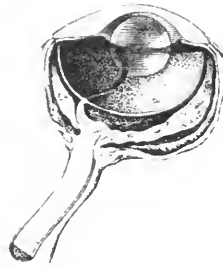
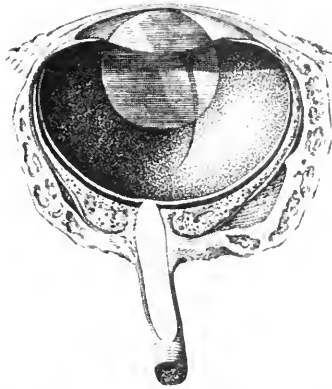
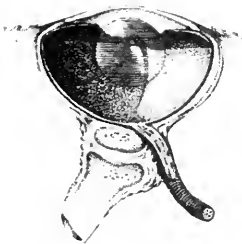
In general, the globe is large, its size tending to vary with the depth at which the animal lives ; as a rule deep-sea fishes are provided with large eyes to receive as much light as possible in these dim regions—until, indeed, the absence of light in benthonic depths leads to the degeneration of the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

¹ p. 722.



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

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

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

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

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

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

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



FIG. 292.—THE EYE OF THE TROUT.

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

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

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

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

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

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

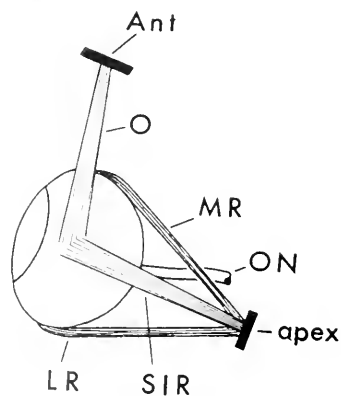


FIG. 293.—THE GENERAL SCHEME OF FISH MUSCLES (SEEN FROM THE DORSAL ASPECT).

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

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

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

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

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

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

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

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

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

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

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

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

² p. 293. ³ p. 234.

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

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

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

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

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

Chondrichthyes (Elasmobranchii)

THE SELACHIAN EYE

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



Pristis

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

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

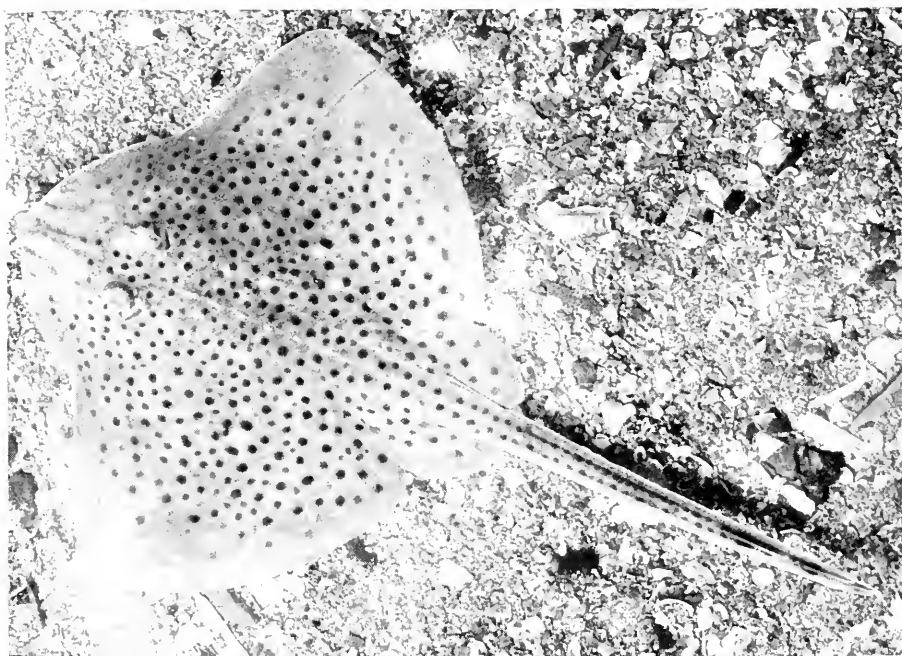
a ciliary zone provided with antero-posterior folds giving rise dorsally to a suspensory ligament of the lens and centrally to a cushion-like papilla provided with an ectodermal protractor lentis muscle ;

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

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

¹ p. 724.

FIGS. 294 TO 296.—TYPICAL SELACHIAN FISHES.

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

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

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

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

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

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

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



Torpedo



Læmargus

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

FIGS. 297 TO 299.—SELACHIAN EYES.

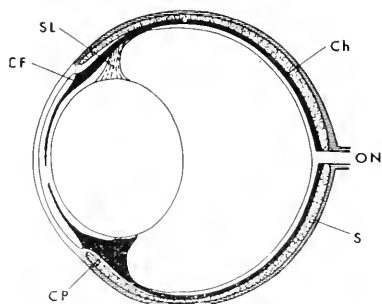


FIG. 297.—Diagram of a Euselachian eye.

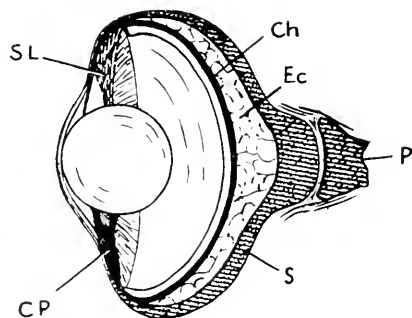


FIG. 298.—Diagram of a Batoid eye.

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

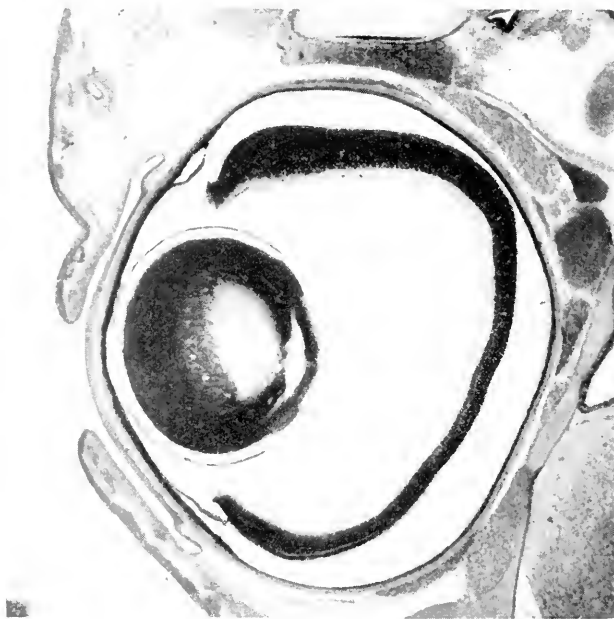
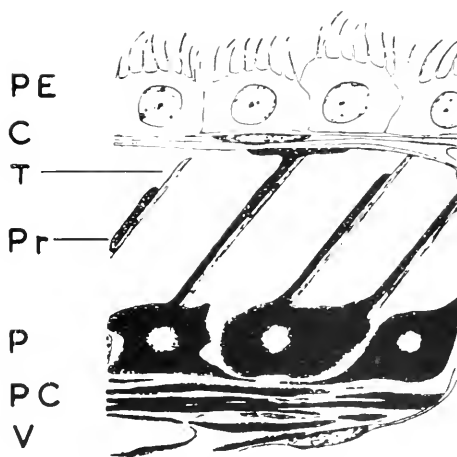


FIG. 299.—The eye of the dogfish.

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

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

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

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

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

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

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

*Lamna*

THE EYE IN EVOLUTION

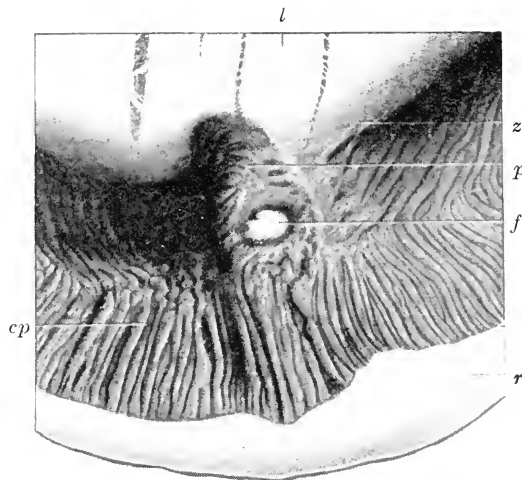
FIGS. 301 AND 302.—THE CILIARY PAPILLA OF THE DOGFISH, *SCYLLIORHINUS*.

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

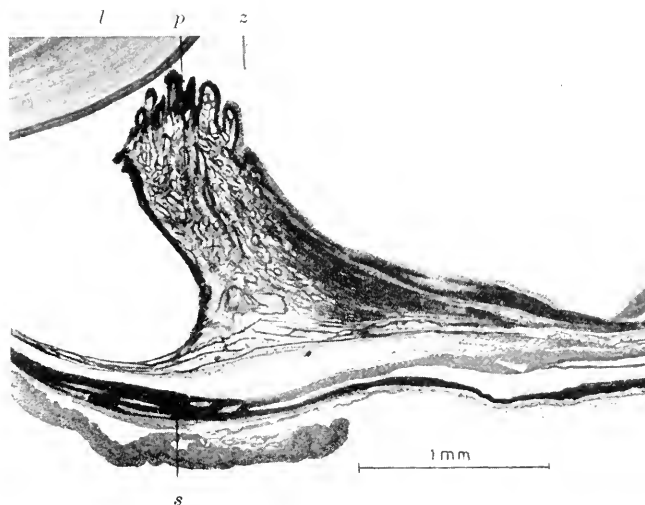
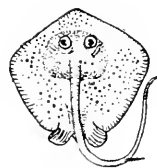


FIG. 302.—Drawing of a section through the ciliary papilla. The papilla, *p*, is seen approximating the lens, *l*. *s*, sclera; *z*, zonular fibres.

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

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

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



Trygon



Mustelus



Squalus

¹ See footnote, p. 267.

² p. 647.

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

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

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



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



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

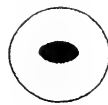


FIG. 305.—The gummy shark, *Mustelus antarcticus*.



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



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



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

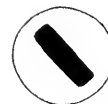


FIG. 309.—The leopard shark, *Triakis*.



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



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



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



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



Heterodontus

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

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

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

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



Scylliorhinus



Raja

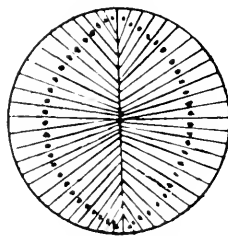


FIG. 314.—LENTICULAR SUTURES OF SELACHIANS.

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

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

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

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

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

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

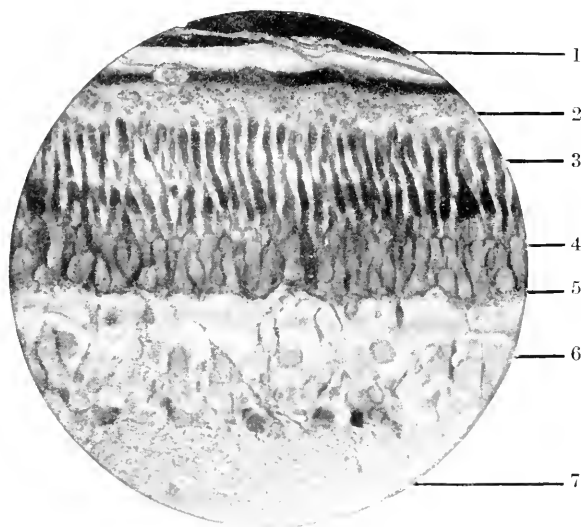


FIG. 315.—THE SELACHIAN RETINA.

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

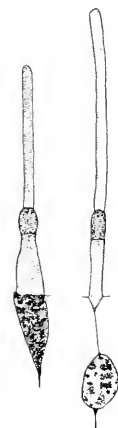


FIG. 316. — THE CONE AND ROD OF THE DOGFISH, *MUSTELUS* ($\times 1000$) (Gordon Walls).

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

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



Squatina

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

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

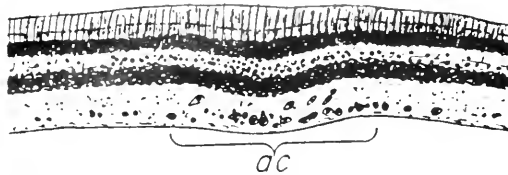


FIG. 317.—THE AREA CENTRALIS (*ac*) OF THE DOGFISH, *MUSTELUS*.

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

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

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

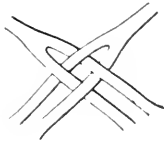


FIG. 318.—The dogfish, *Squalus*.

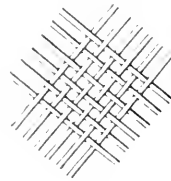


FIG. 319.—The skate, *Raja*.

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

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

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

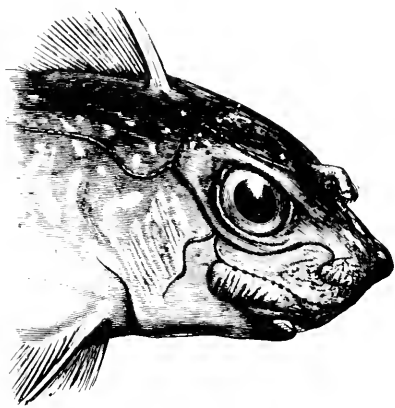


FIG. 320.—The head of the rabbit-fish, *Chimera monstrosa* (Bland-Sutton's *Lectures and Essays*, Heinemann).

THE HOLOCEPHALIAN EYE

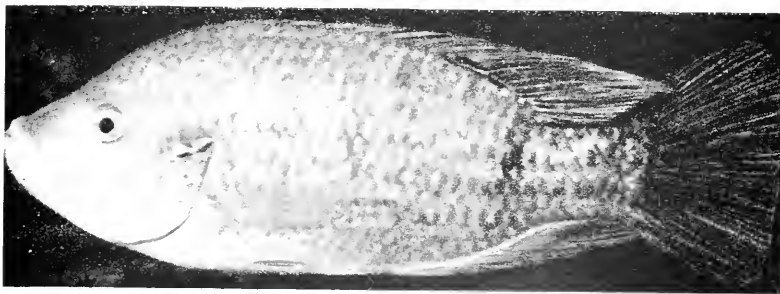
THE HOLOCEPHALIANS are represented today only by the Chimæras (rabbit-fishes or ghost-sharks), somewhat shark-like fish of wide distribution and very primitive in type (Fig. 320) ; they are all deep-sea bottom fishes, and their eyes, which are of the same type as the selachian eye, are remarkable for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

Osteichthyes

THE TELEOSTEAN EYE

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

FIGS. 321 AND 322.—TYPICAL TELEOSTEAN FISHES.

FIG. 321.—The carp, *Cyprinus* (photograph by Michael Soley).FIG. 322.—The mouth-breeder cichlid, *Cichla* (Zool. Soc., London).

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

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

a very elaborately developed annular ligament bridging the angle of

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

the presence of a choroidal gland in most species ;

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

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

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

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

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

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

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



Carassius

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

¹ p. 332.

² p. 722.

³ p. 736.

⁴ p. 403, Fig. 496.

FIGS. 323 AND 324.—THE TELEOSTEAN EYE.

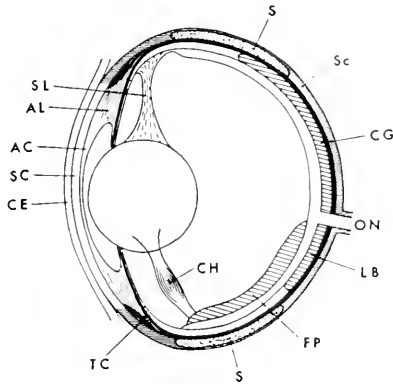


FIG. 323.—Diagram of a Teleostean eye.

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

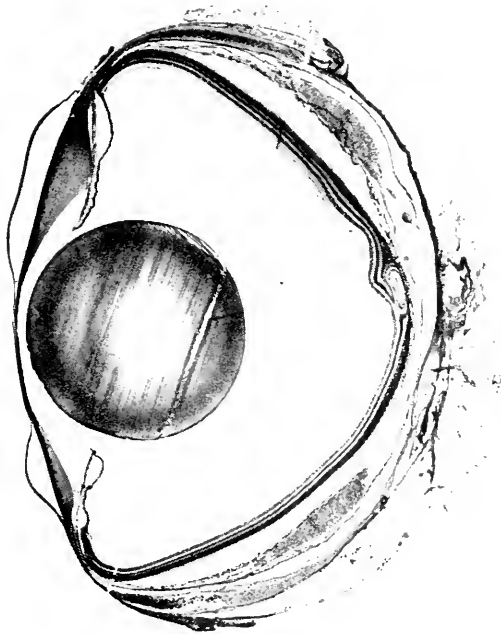


FIG. 324.—The eye of the trout. In the section the dermal layer of the cornea has come loose, as usually occurs (Norman Ashton).



Mormyrid

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

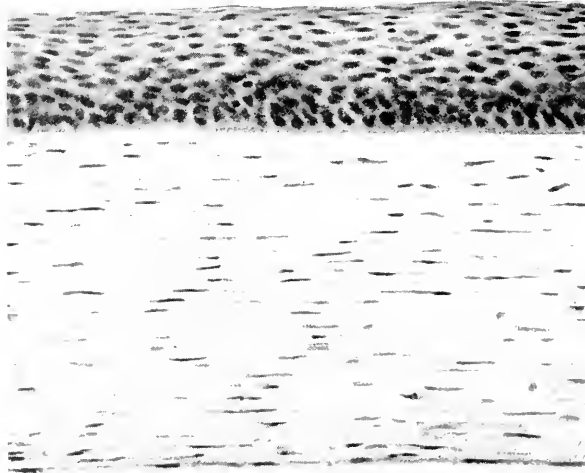


FIG. 325—THE CORNEA OF THE CARP.
Showing the thick epithelium (Smelser and Chen).

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

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

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

*Xiphias**Thunnus*

Minnow

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

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

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

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

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

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

¹ p. 265.

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

³ p. 326, Fig. 386.

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

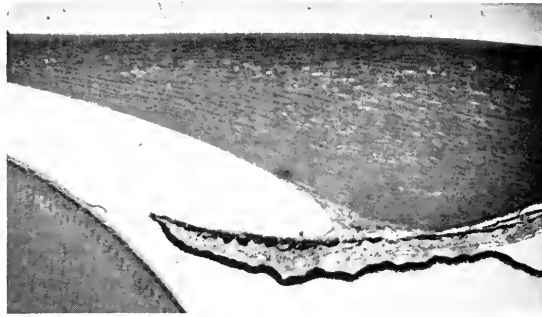


FIG. 326.—THE ANGLE OF THE ANTERIOR CHAMBER OF THE TROUT.

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



Gobioides

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

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

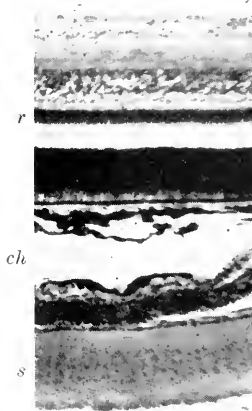


FIG. 327.—SECTION THROUGH THE EQUATORIAL SEGMENT OF THE EYE OF THE TROUT.

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

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

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

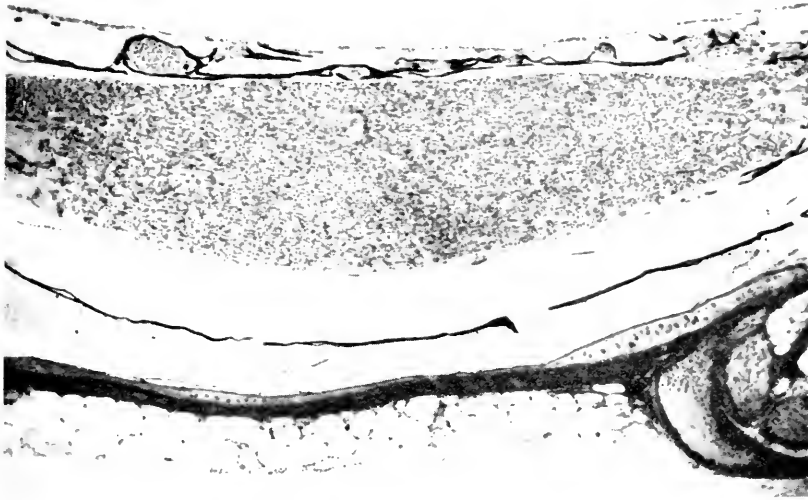


FIG. 328.—The "gland" occupies the upper part of the figure ($\times 80$).

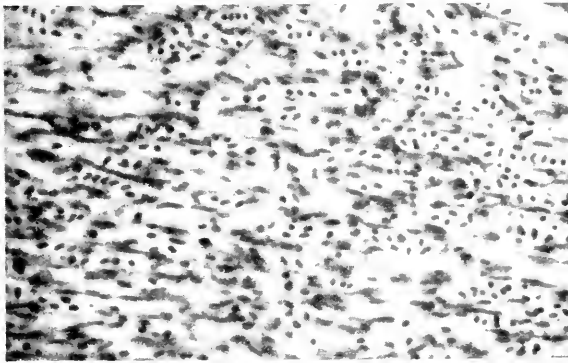


FIG. 329.—Structure of the "gland" ($\times 320$).

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

¹ p. 457.

THE EYE IN EVOLUTION

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

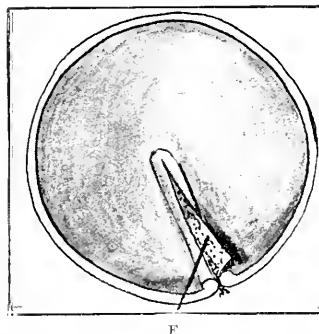


FIG. 330.—The macroscopic intra-ocular appearance of the posterior half of the globe seen from the front. F, falciform process.

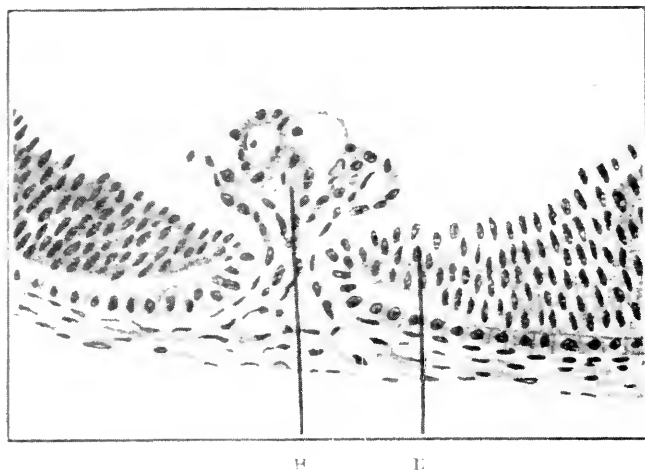


FIG. 331.—Section across the region of the fetal fissure. H, vascular mesoderm of the falciform process; E, neuro-ectoderm of the wall of the optic cup (Mann, after von Szily).

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

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

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

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

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

*Anguilla*

Cat-fish

*Gadus**Clupea harengus*

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

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

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

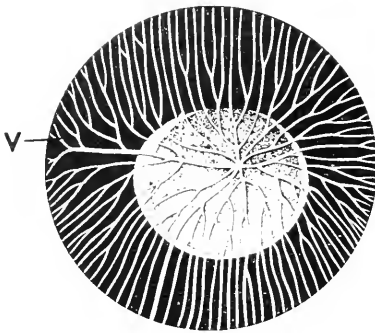


FIG. 332.—In the goby fish, *Gobius pacilichthys*. The vessels emanate from the central artery of the retina and run over this tissue within the vitreous. The division of the principal vessel into the annular vein is seen on the nasal side, at V (after Karsten).



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

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



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

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



FIG. 335.—THE RETINA OF THE EEL.

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

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

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

¹ See footnote p. 267.

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

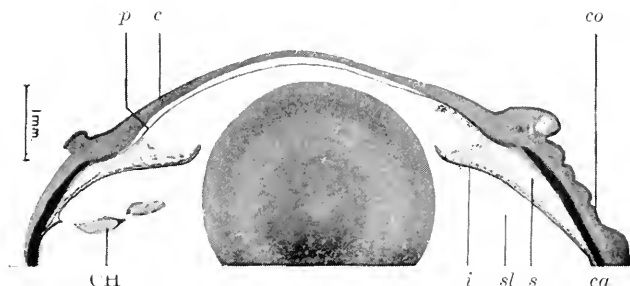


FIG. 336.—THE ANTERIOR SEGMENT OF THE EYE OF THE BULL-HEAD, *COTTUS BUBALIS*.

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

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

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



Scorpena

PLATE II
THE IRIDES OF TELEOSTS (Ida Mann)

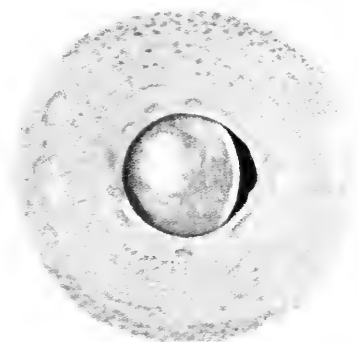


FIG. 1.—The killifish, *Aplocheilichthys rubrosignata*.

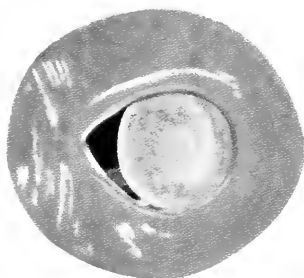


FIG. 2.—The salmon, *Salmo salar*.

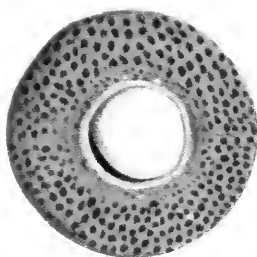


FIG. 3.—The telescope-eyed goldfish, *Carassius*.

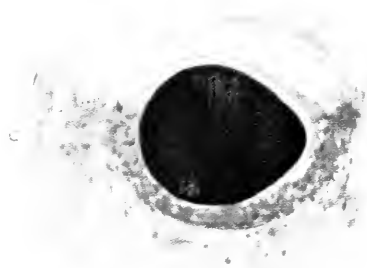


FIG. 4.—The red-eyed fish, *Tetraodon lineatus*.
C, ciliary arteries.



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

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

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



Beryx

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



Xiphias

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

¹ p. 646.

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

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

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



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

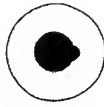


FIG. 338.—The sailfish, *Istiophorus*.



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



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

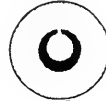


FIG. 341.—The cat-fish, *Plecostomus*, showing the operculum in various stages of closure of the pupil.

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

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

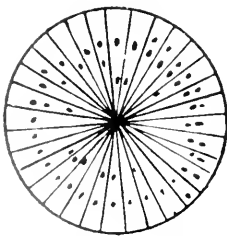


FIG. 342. — LENTICULAR SUTURES OF TELEOSTS.

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

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

¹ p. 325.

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



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

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

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

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

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

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

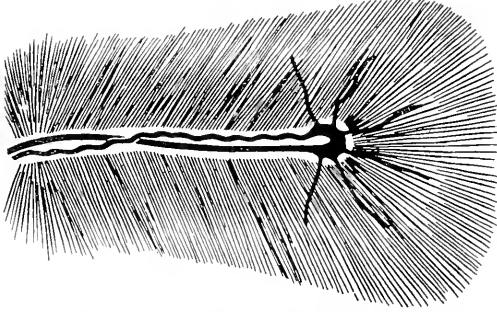


FIG. 344.—The cod, *Gadus*, showing the vessels of the falciform process running over the elongated optic disc and breaking up into 6 branches of the hyaloid artery (after Beauregard).

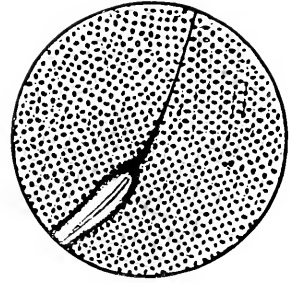


FIG. 345.—The scorpion fish, *Scorpaena*, showing the optic nerve entrance in relation to the falciform process and the peculiar mosaic arrangement of the background of the fundus (after Franz).

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

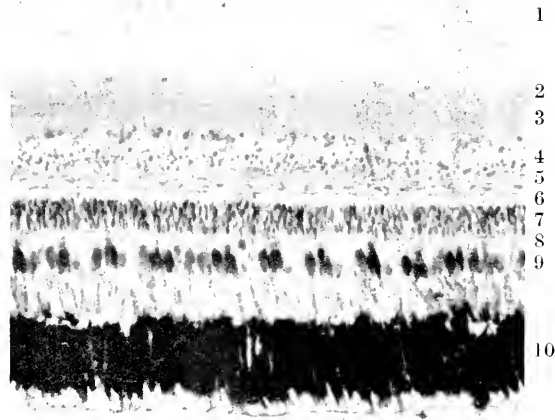


FIG. 346.—THE RETINA OF THE TROUT, *SALMO TRUTTA*.

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

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

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



Ameiurus

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

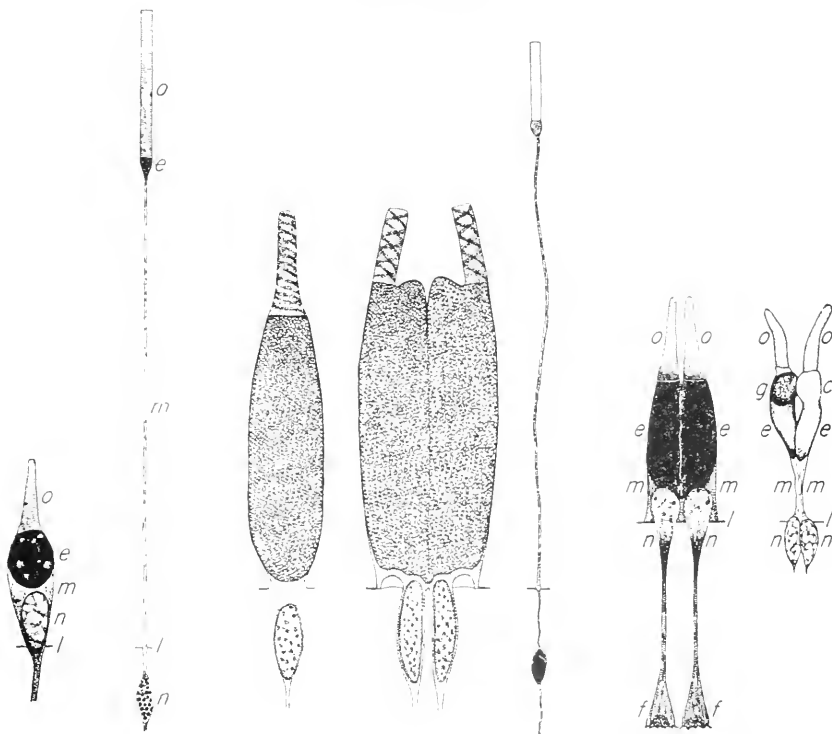


FIG. 347.

FIG. 348.

FIG. 349.

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

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

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

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

*Fundulus*

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

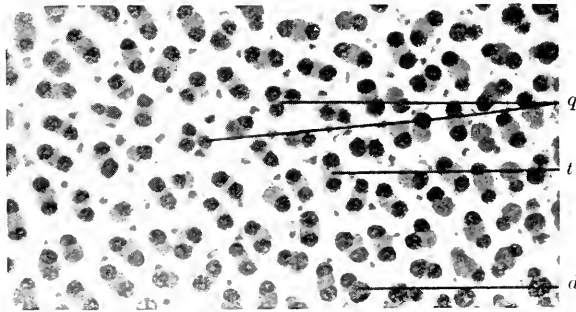


FIG. 350.—TRIPLE AND QUADRUPLE CONES IN A TELEOSTEAN FISH.

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

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

*Salmo trutta*

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

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

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

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

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

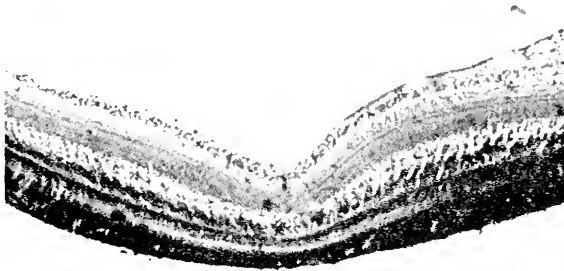


FIG. 351.—Section through the fovea of the blenny, *Blennius*.

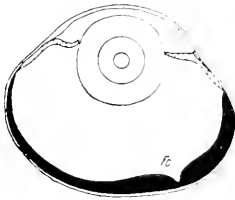


FIG. 352.—The fovea, *Fo*, of the sea-horse, *Hippocampus*.

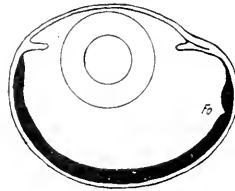


FIG. 353.—The fovea, *Fo*, of the sea-bass, *Serranus* (Kahmann, v. Graefes *Arch. Ophthalm.*).

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



Syngnathus

¹ p. 253.

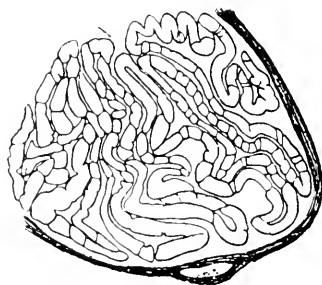
*Blennius**Bathylagus*

FIG. 354.—THE OPTIC NERVE OF TELEOSTS.

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

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

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

*Hippocampus**Misgurnus*

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

² See, also, pp. 365, 382, 486.

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

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

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

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

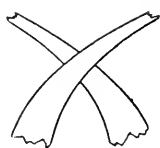


FIG. 355.—The usual configuration: the simple crossing of intact nerves.



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

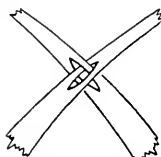


FIG. 357.—The parrot-fish: the interlacing of bundles.

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

¹ p. 289.

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

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

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

THE DIPNOAN EYE

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

FIGS. 358 TO 360.—EXTANT DIPNOAN FISH.



FIG. 358.—*Protopterus*.



FIG. 359.—*Lepidosiren*.

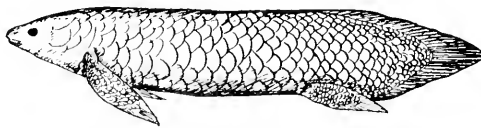


FIG. 360.—*Neoceratodus*.

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

¹ p. 266.

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

The retina shows several peculiarities. The cells of the pigimentary

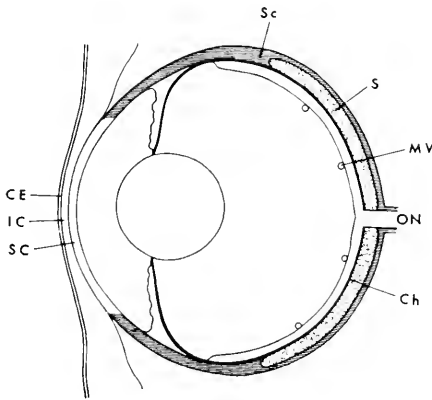


FIG. 361.



FIG. 362.

FIG. 361.—Diagram of a Dipnoan eye.

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

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

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

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

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



FIG. 363.—A PIGMENT CELL.

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

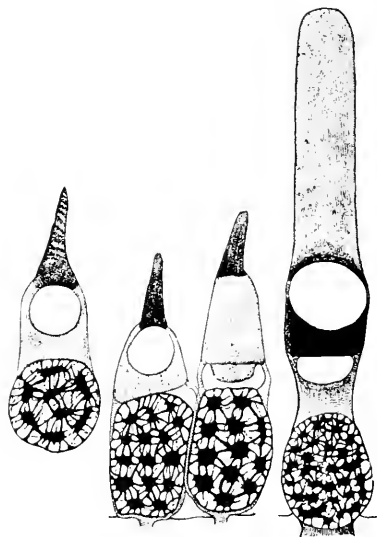


FIG. 364.—A SINGLE CONE, A DOUBLE CONE AND A ROD.

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

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

THE COELACANTH EYE

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

¹ See also snakes, p. 392.

² p. 234.

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

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

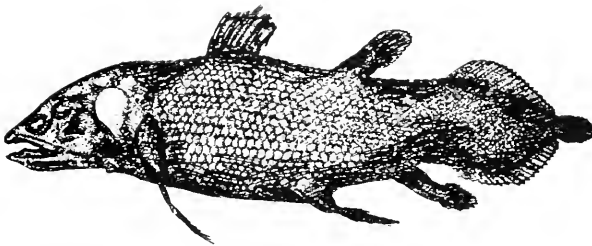


FIG. 365.—THE COELACANTH, *LATIMERIA CHALUMNAE*.
(1 16 natural size) (after Günther and Deckert).

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

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

THE CHONDROSTEAN EYE

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



Polyodon

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

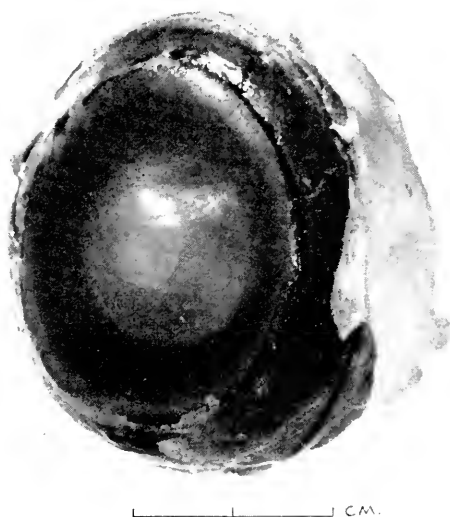


FIG. 366. The general configuration of the eye showing the short antero-posterior diameter, the large cornea through which the lens is visible, and the peri-corneal ring of calcified scleral plaques.

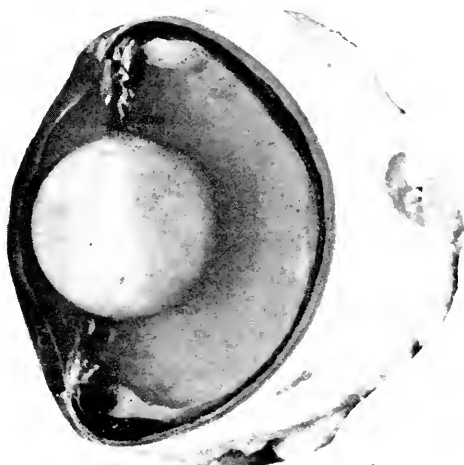


FIG. 367.—Section of the eye showing the large spherical lens lying close to the cornea.

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

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

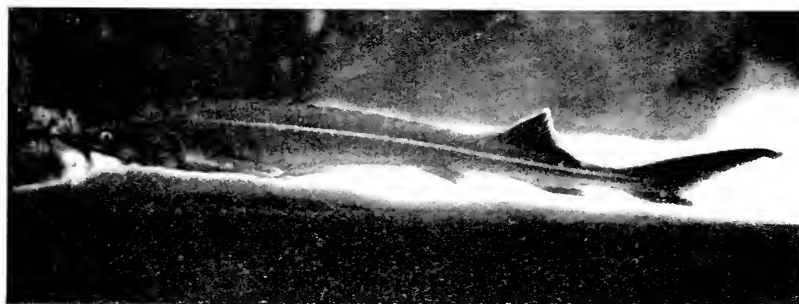


FIG. 368.—THE STERLET, *ACIPENSER RUTHENUS* (Zool. Soc., London).

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

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

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

¹ p. 234.

² p. 609.

THE EYE IN EVOLUTION

FIGS. 369 AND 370.—THE CHONDROSTEAN EYE.

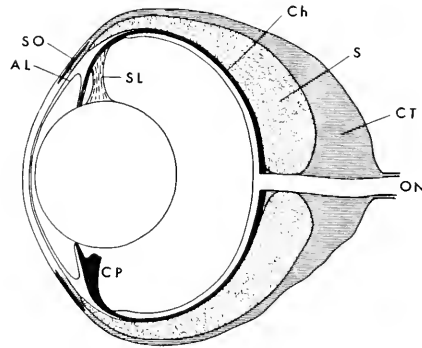
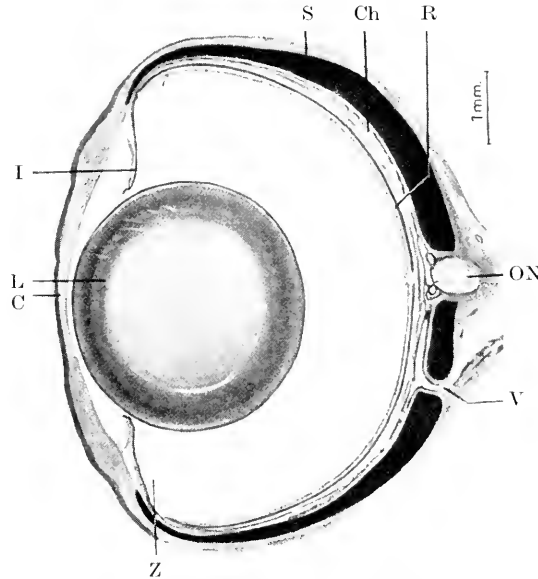


FIG. 369.—Diagram of a Chondrostean eye.

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

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

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

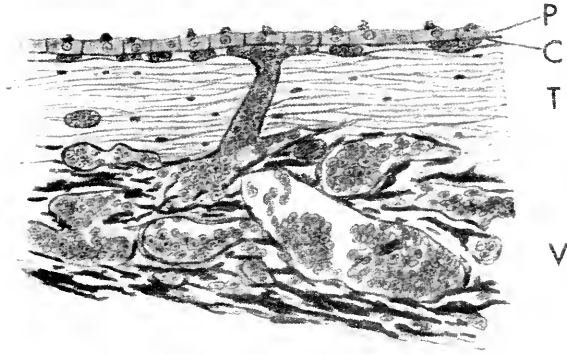
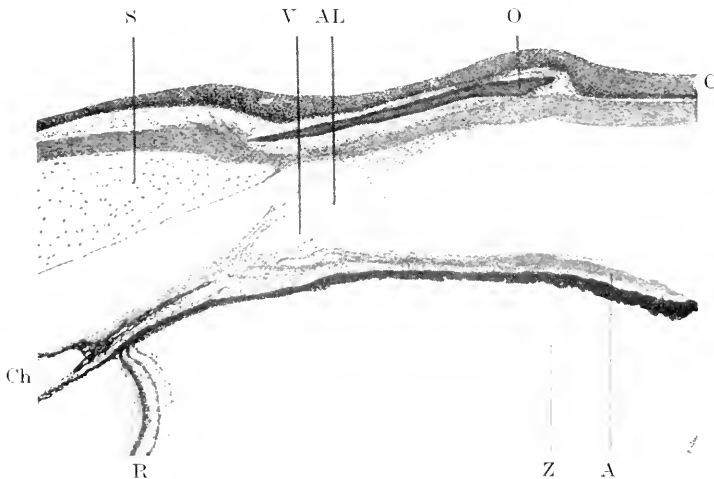


FIG. 371.—THE TAPETUM OF CHONDROSTEANS.

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

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

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

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

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

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

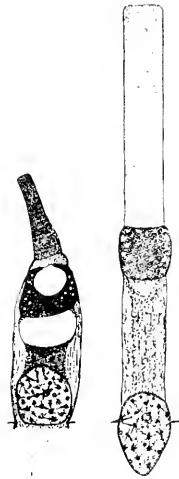


FIG. 373. — THE VISUAL ELEMENTS OF *ACIPENSER FULVESCENS*.

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

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



Polypterus



Calamoichthys

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

¹ p. 321.

THE HOLOSTEAN EYE

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

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

FIG. 374.



FIG. 375.

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

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

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

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

ANOMALIES IN THE EYES OF FISHES

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

THE TUBULAR OR TELESCOPIC EYE

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

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

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

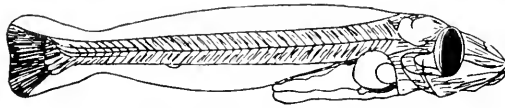


FIG. 376.—In the larva the eye is directed forwards.

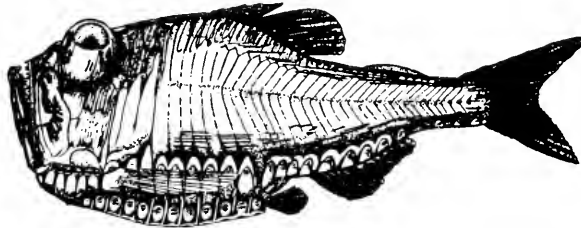


FIG. 377.—In the adult the eyes are tubular and upward-looking ; the body is covered with luminous organs giving the scales a silvery gleam (compare Fig. 892) (after Goode and Bean).

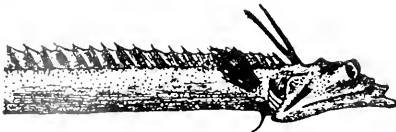


FIG. 378.—*Stylophorus paradoxus*. An inhabitant of the deep Atlantic. The eyes are directed forwards and slightly upwards (after Goode and Bean, 1896).



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

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

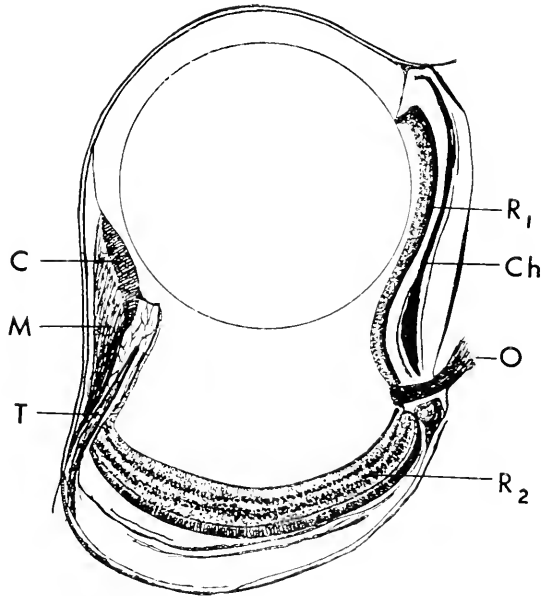


FIG. 380.—THE TUBULAR EYE OF A DEEP-SEA FISH.

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

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

*Opisthoproctus*

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

The intimate structure of such an eye is seen in Fig. 380. The principal retina is well formed, the accessory retina atrophied, while the optic nerve emerges laterally between the two. To move the immense lens there is a lens pad controlled to some extent by muscles which enable the eye to be focused on a distant object. On the whole, however, such eyes are myopic and specifically adapted for the perception of the small amount of light available, although it is possible that a sufficiently adequate image of prey may be appreciated to allow its capture when it approaches so closely that it can be snapped at.



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

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

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

THE AMPHIBIOUS EYE

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

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

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



FIG. 382.

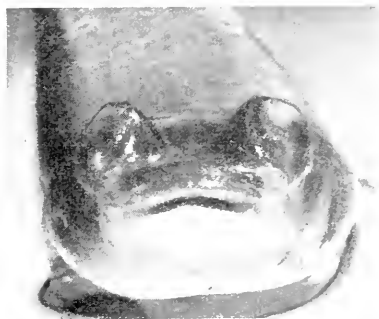


FIG. 383.



FIG. 384.

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

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

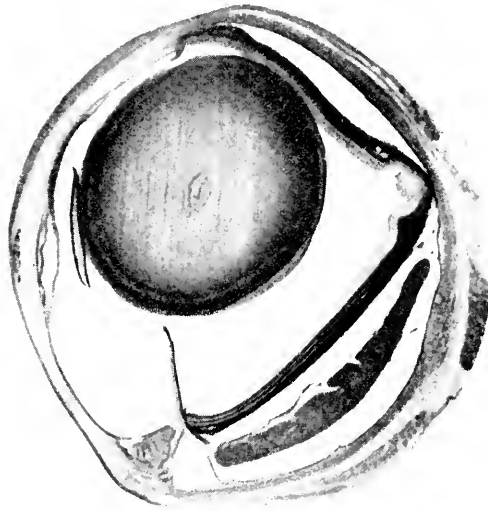


FIG. 385.—THE EYE OF *AVABLEPS* IN VERTICAL SECTION.

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

STALKED EYES

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

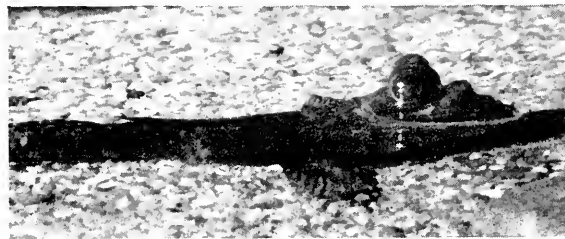


FIG. 386.—THE MUD-SKIPPER, *PERIOPHTHALMUS*.

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

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

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

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

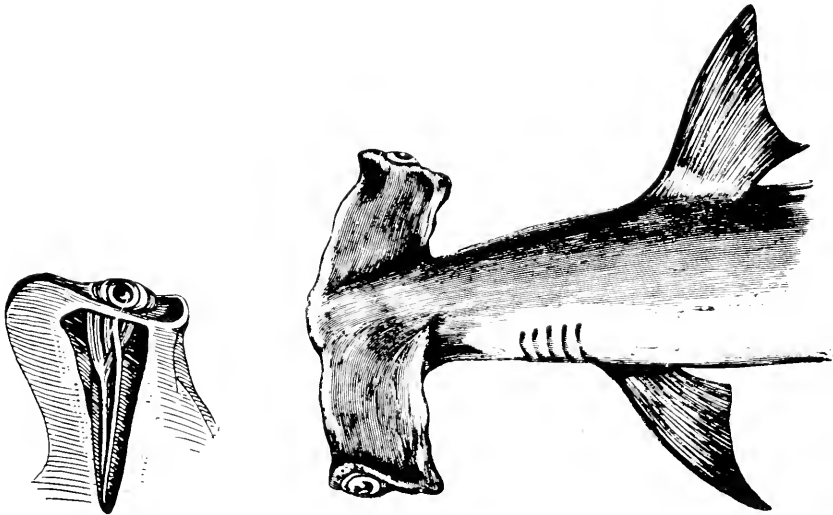


FIG. 387.

FIG. 387.—The dissected orbit.

FIG. 388.

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

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

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



Sphyrna tiburo

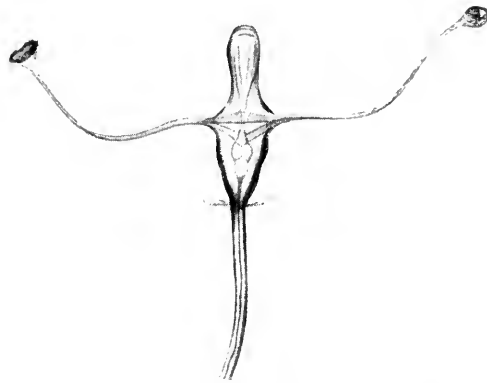


FIG. 389.—THE STALKED-EYED TELEOST, *STYLOPHTHALMUS PARADOXUS*, THE LARVA OF *IDIACANTHUS*.

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

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

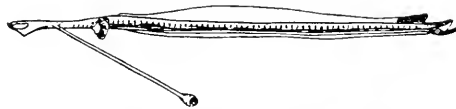


FIG. 390.—Young stalk-eyed larva, *Stylophthalmus paradoxus*, 16 mm. long.



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

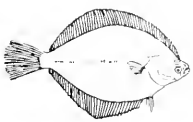


FIG. 392.—Adult male *Idiacanthus*.

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

THE MIGRATORY EYE

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



Plaice



Sole

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

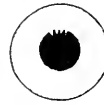
*Psettodes*

FIG. 393.



FIG. 394.

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

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

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¹ p. 679.² p. 287.

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FIG. 395.—ANDRÉ-JEAN-FRANÇOIS ROCHON-DUVIGNEAUD (1863-1952).

CHAPTER XII

THE EYES OF AMPHIBIANS

One of the most interesting figures associated with the study of the eyes of Vertebrates was ANDRÉ-JEAN-FRANÇOIS ROCHON-DUVIGNEAUD (1863–1952) (Fig. 395). Born in the Dordogne, he studied medicine in the Faculté de Bordeaux and in 1889 became an interne des Hôpitaux de Paris at the Hôtel Dieu and a Chef de Clinique in 1895. A clinician and operator of repute, he contributed a number of excellent papers to ophthalmic literature, but he was always interested in anatomy. His doctorate thesis (1892) was on the anatomy of the angle of the anterior chamber and the canal of Schlemm—a historic paper. His anatomical researches on the human eye led him to study the eyes of animals and from 1916 onwards numerous papers on this subject full of painstaking and careful observations of unusual originality and exactitude appeared from his pen. A study of these papers reveals even to the casual reader the delight it must have given him to produce them, and it is not surprising that he retired from clinical practice in 1926 and devoted all his time, working in a small laboratory at his home, to the study of the eyes of various species and spending much energy in observing the habits of animals in all the parts of France. His numerous papers on comparative anatomy were collected together in his classical textbook, *Les Yeux et la Vision des Vertébrés* (1943), and earned him a well-deserved international reputation. Nor was he without honour in his own country, having been elected to the Académie de Médecine in France in 1940. At his death it was truly written: “*Homme droit, désintéressé, serviable, c’est un grand savant modeste qui disparaît.*”

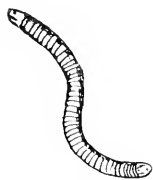
AMPHIBIA (ἀμφίβιον, double life) mark the transition from aquatic to terrestrial life. The early forms found in upper Devonian strata and probably, as we have seen,¹ sprung from the lobe-finned Crossopterygians, are extinct. In Carboniferous times² these reached their prime and some species attained a gigantic size; today relatively few types are extant and these, usually small in size and sluggish in habit, generally live near the water's edge. The main features wherein they differ from fishes are determined by their life on land—the disappearance of the gills in adult life, the development of lungs (with a three-chambered heart) from the air-bladder, the transformation of the lobed fins into digital limbs, the (usual) loss of the scaly exoskeleton, the adaptation of the ear to aerial vibrations and of the eye to aerial vision.

The surviving members of this once populous class are divided into three orders:

1. APODA (ἀ, without; ποῦς, ποδός, a foot) (or GYMNOPHIONA, γυμνός, naked; ὄφιόεος, serpent-like), a peculiar archaic worm-like type without limbs and of burrowing habit, are found in the mud-banks of tropical countries. They are

¹ p. 235.

² p. 754.



Cæcilian

represented by the CÆCILIANs (*cæcus*, blind) and a number of related species in all of which the eyes are degenerate; they will therefore be discussed subsequently.¹

2. URODELA (*οὐρά*, tail; *δῆλος*, visible) (or CAUDATA, *cauda*, a tail), tailed Amphibians, typified in the salamanders and the newts, are generally divided into 7 families. Of these several are cavernicolous in habit, having little use for eyes; these are therefore often degenerate and are discussed at a later stage (*Proteus*, etc.).² Others, such as the newts (*Triturus*), *Ambystoma*, and the terrestrial salamanders, have relatively simple but well-formed eyes.

3. ANURA (*ἀ*, privative; *οὐρά*, tail) or tail-less Amphibians, consisting of nearly 1,000 different types including the common frog (*Rana*), the toad (*Bufo*), the tree-frog (*Hyla*), the obstetric toad (*Alytes*), the Surinam toad (*Pipa*), the African clawed toad (*Xenopus*) and some other species, have well-developed eyes.

The general characteristics of the amphibian eye as seen in the last two orders are as follows:

The transition from water to air and the consequent lack of the necessity for streamlining the globe, allow it to assume a spherical shape. Moreover, the difference in refractivity between the air and the cornea allows this structure to assume a new role in the dioptrics of the eye; it therefore becomes highly arched and its optical properties are good. The lens can therefore fall backwards from the cornea; it still, however, remains large and is moved as a whole, thus retaining an accommodative mechanism somewhat resembling although not analogous with that seen in fishes.

The visual elements are complex and relatively gross—two types of rods and single and double cones reminiscent of those occurring in Holosteans and Dipnoans.

To protect and moisten the cornea, lids are provided, together with a harderian gland and a naso-lacrimal duct.

THE ANURAN EYE

THE EYE OF THE FROG (*Rana*) has probably received more detailed study than that of any Vertebrate other than man (Figs. 397–8).³ The GLOBE is almost spherical, the *cornea* and the *sclera* maintaining the same curvature. The latter, after metamorphosis from the tadpole stage, develops on its inner aspect a cup of hyaline cartilage, thickest at the posterior pole and extending anteriorly to beyond the insertions of the rectus muscles; it is pierced by the foramen for the optic nerve as well as by small canals which allow the passage of the ciliary vessels and nerves (Caso, 1931; Yamasaki, 1952). In some tree-frogs (Hylidæ) the scleral cartilage is discontinuous or lacking;

¹ p. 730.

² p. 728.

³ Dating from the description of Petit (1737) and Soemmerring (1818). See Gaupp (1846), Tretjakoff (1906), Walls (1942), Rochon-Duvigneaud (1943). For development, see Trep (1906), Studnicka (1913), Jokl (1918–20).

and in one species it is replaced anteriorly by a ring of bone (*Hypopachus incassatus*). The cornea in the larval stage has the duplex form of many fishes, with the dermal portion separate from the scleral; fusion, however, takes place in the adult so that the fully metamorphosed structure has the typical vertebrate characteristics of a regularly-layered epithelium, a homogeneously stratified substantia propria and Descemet's membrane with its tenuous endothelium.

The *uveal tract* is well developed (Fig. 399). The choroid consists essentially of a choriocapillaris external to which the heavily pigmented tissue is divided into two strata separated by a layer of large veins, traversed by broad pigmented bands running obliquely (the *vascular layer* of Gaupp, 1904); there is no true argentea or tapetum, but a

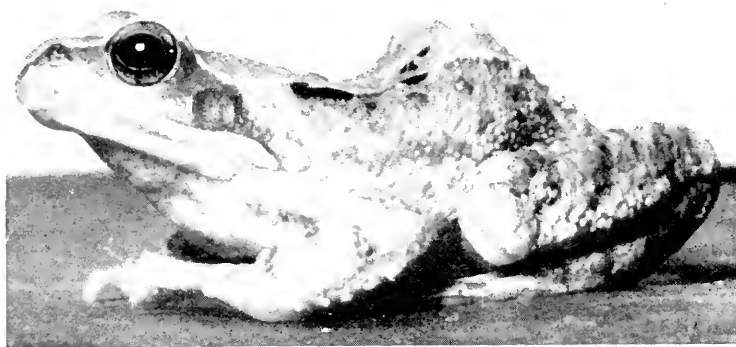


FIG. 396.—THE FROG, *RANA*.

The disc-shaped patch behind and below the eye marks the position of the ear.

certain degree of "eye-shine" is contributed by cells containing a carotenoid yellow pigment and others with crystals of guanine.

The *ciliary body* is well-formed and triangular in shape. On the internal aspect the double layer of epithelium is plicated into numerous meridional ciliary folds running anteriorly to the back of the iris and from these the fibres of the zonule take origin (Teulière and Beauvieux, 1931). Dorsally and ventrally these folds are hypertrophied, two or three neighbouring folds dorsally, a single fold ventrally, and in most species are continued to the pupillary margin where they thicken to form the dorsal and ventral pupillary nodules: their function may be to keep the iris away from the lens and thus to allow the aqueous humour to flow backwards when the lens is drawn forwards in accommodation (v. Hess, 1912). The mass of the triangular ciliary body is occupied by a meshwork of vascularized pigmented tissue; and from the scleral aspect of the triangle in the dorsal and ventral regions a ciliary muscle (or tensor choroideæ) forms two crescentic slips of

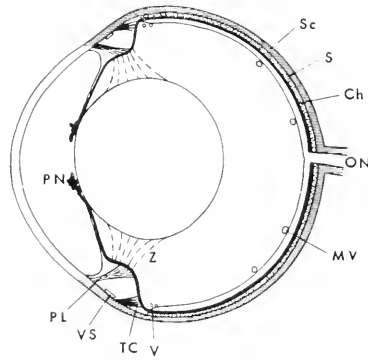
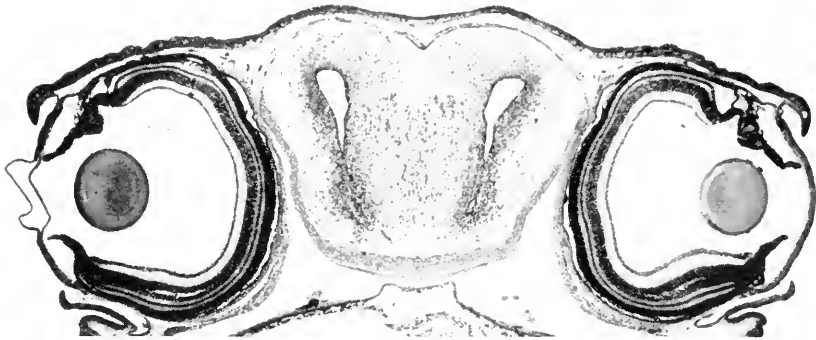


FIG. 397.—DIAGRAM OF AN ANURAN EYE.

Ch, choroid; MV, membrana vasculosa retinae; ON, optic nerve; PL, protractor lentis muscle; PN, pupillary nodule; S, scleral cartilage; Sc, sclera; TC, tensor choroideæ; V, hyaloid vein; VS, ciliary venous sinus; Z, zonule.

FIG. 398.—SECTION THROUGH THE HEAD OF THE FROG TO SHOW BOTH EYES ($\times 20$) (Norman Ashton).

meridional smooth fibres running backwards to be inserted into the choroid. This muscle is discontinuous and is absent in the lateral segments of the globe. In the same two regions a ciliary venous sinus, reminiscent of a canal of Schlemm, forms two discontinuous crescents, a dorsal and a ventral, situated between the sclera and the ciliary body, connecting the veins of the iris with the subconjunctival veins (Tretjakoff, 1906). Also in the same two regions there are two protractor lentis muscles (Tretjakoff, 1906) of mesodermal origin supplied by a branch of the 3rd nerve. Each, the dorsal and the ventral, arises from the corneal margin, enters the ciliary triangle and is inserted into the hypertrophied ciliary processes. These by traction on the annular fibres pull the lens forward in accommodation, approximating its structure to the cornea as in Selachians (Figs. 400-1).

The *iris* is thin and delicate (Plate III). Both retinal layers are pigmented and an ectodermal sphincter and dilatator of myo-epithelial cells are present (Grynfeltt, 1906 ; Tretjakoff, 1906). The stroma is thickly packed with melanophores as well as with cells containing yellow, brown and copper-coloured carotenoid pigments often associated with a metallic sheen due to the presence of guanine crystals. As a result the iris is usually brilliantly coloured, as if dusted with a golden or bronze powder so that it simulates the lustrous appearance of old gold or Chinese lacquer¹ (Millot, 1923 ; Mann, 1931). It is often coloured similarly to the skin of which at first glance it appears to be an integral part. An almost constant feature is a vertical stripe often associated with a groove running downwards from the lower pupillary margin to

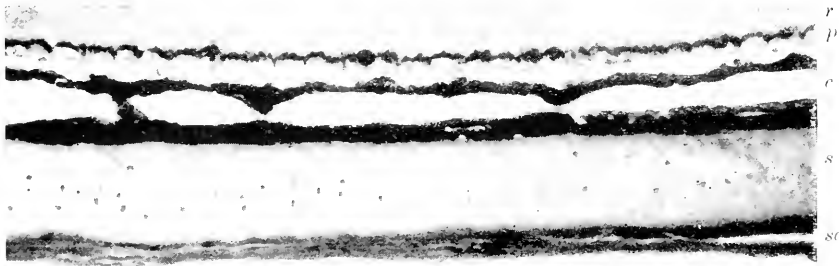


FIG. 399.—THE OCULAR COATS OF *RANA*.

Showing the rods and cones, *r*: the pigmentary epithelium, *p*: the choroid, *c*, divided into two strata: the scleral cartilage, *s*: and the sclera, *sc* ($\times 200$) (Norman Ashton).

the periphery of the iris where it ends, presumably a relic of the foetal cleft (Johnson, 1927 ; Mann, 1931).² The vessels of the iris are arranged in the same general plan as those of Fishes: several superficial arteries run irregularly and circumferentially on the surface taking a tortuous course towards the pupil and draining into veins which run in a radial course but lie at a deeper level and are thus usually hidden by the heavy pigmentation (Mann, 1929-31) (Plate III ; Fig. 402). In the primitive clawed-toad, *Xenopus*, all the vessels are obscured by pigment.

¹ Some of the colours seen are brilliant and quite beautiful—gold and brown spots on chocolate in the edible frog, *Rana esculenta*; red and green dots in the American bull-frog, *R. catesbeiana*; a chocolate stripe across a gold and brown background in the Malayan bull-frog, *Kaloula pulchra*; gold speckled in russet in the tree-frog, *Hyla*, as also in the giant toad, *Bufo marinus*; gold and brown in the common toad, *Bufo bufo*; a brilliant metallic green in the green toad, *B. viridis*; green and silver with a horizontal stripe of brown in the S. American toad, *B. arenarum*; and so on.

² Such a pigmented furrow or ridge, sometimes associated with a pupillary notch is seen in certain teleostean Fishes (herring, trout, minnow, orfe, cod, carp, etc.), rarely in Reptiles (the Bengal monitor, *Varanus bengalensis*, and *Iguana tuberculata*), and never in Urodeles.



Xenopus



FIG. 400.—THE CILIARY REGION OF THE FROG, *RANA* ($\times 126$) (Norman Ashton).

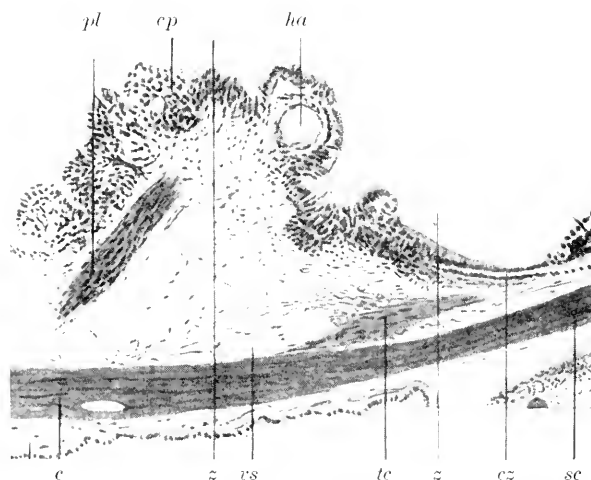


FIG. 401.—THE CILIARY REGION OF THE FROG, *RANA*.

A radial section through the inferior part of the eye. *c*, cornea; *cp*, ciliary process; *cz*, ciliary zone; *ha*, hyaloid artery penetrating the region of the ciliary process; *pl*, protractor lentis muscle; *tc*, tensor choroideae; *vs*, ciliary vein; *z*, region of zonular attachment (Rochon-Duvigneaud, *La Vision des Vertébrés*, Masson et Cie, Paris).

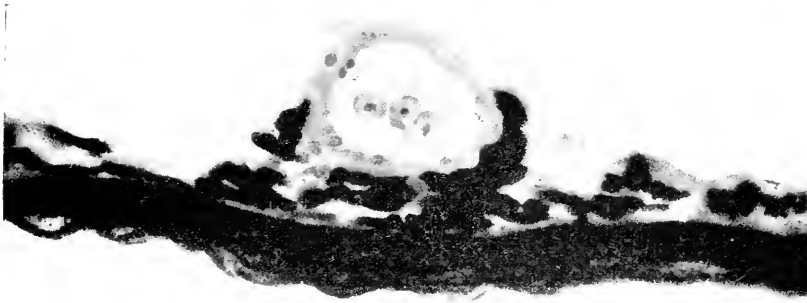


FIG. 402.—THE IRIS OF THE FROG, *RANA*.
Showing a large superficial artery ($\times 500$) (Norman Ashton).

The *pupil* is usually circular in dilatation but on contraction takes on varied shapes, sometimes round (*Pipa*), usually horizontally oval (*Rana*), occasionally forming a vertical lozenge-shaped slit (the spadefoot toad, *Scaphiopus*, *Phrynomerus*, *Alytes*, *Hyla*, etc.) (Boulenger, 1896 ; Johnson, 1927 ; Mann, 1931 ; and others) (Fig. 403). Other irregular shapes occur, such as the heart-shaped pupil of the fire-bellied toad, *Bombinator*, the diamond-shaped pupil of the large-fingered frog, *Rana halcina*, the semicircular pupil with the flat side uppermost of the bull-frog, *R. catesbiana*, or the pear-shaped pupil of *Pelobates* (Figs. 403 and 404). The pupils retain some of the autonomous activity characteristic of Fishes, contracting on the direct stimulation of light, and for this purpose the sphincter is heavily pigmented so that its



Pipa



Bombinator
in warning
attitude

FIGS. 403 AND 404.—ANURAN PUPILS.

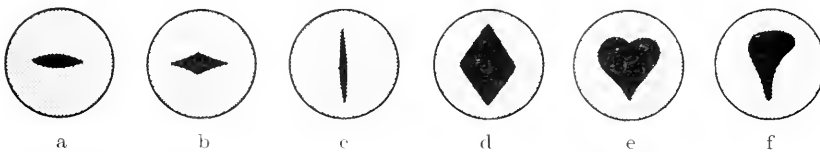


FIG. 403.—The typical pupils of various Amphibians in the contracted state (right eye) ; when dilated all are circular. (a) The Javanese flying frog, *Polypedates reinwardti* ; (b) *Trachycephalus* ; (c) the obstetric frog, *Alytes obstetricans* ; (d) *Hyla vasta* ; (e) the fire-bellied toad, *Bombinator* ; (f) *Pelobates fuscus*.

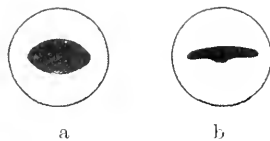


FIG. 404.—The dilated (a) and contracted (b) pupil of the green tree frog, *Hyla corruca*.

myo-epithelial cells will absorb a considerable amount of light-energy ; indeed, contraction occurs in the excised eye (Brown-Séquard, 1859 ; Steinach, 1890 ; Magnus, 1899 ; Guth, 1901), the effect being most marked in the blue region of the spectrum (Weale, 1956, in *Rana temporaria* but not in *Xenopus*). Ordinarily, however, this action is masked by the nervous reflex action which originates from retinal activity.

Amphibians are the first among Vertebrates wherein the movements of the pupil are mediated by a neural mechanism, but although their pupils are more actively motile than those of Fishes, their movements remain sluggish for the sphincter muscle is still comparatively weak. Thus the oval pupil of the common frog requires the stimulus of an increase of light-intensity of 200 times to induce a contraction to $\frac{1}{3}$ of its size from full dilatation.

The *lens* in the tadpole, like that of Fishes, is spherical and approximates the cornea ; in the adult frog it moves posteriorly leaving a deep anterior chamber and becoming somewhat flattened in an antero-posterior direction (axial : equatorial diameter, 1: 1.3, Rabl, 1898) (Fig. 398). The large nucleus is dense and the periphery soft and elastic, the internal structure and the epithelium conforming to the usual vertebrate plan with a vertical suture anteriorly and a short horizontal suture in the posterior part, as in selachian fishes (Fig. 314).

The *blood supply* to the eye has several points of interest and has been studied by H. Virchow (1881), Tretjakoff (1906), Grynfeldt (1907), and Kutsukaka (1952). It is derived from the ophthalmic artery, a branch of the internal carotid. From this artery two posterior ciliary branches are given off which enter the eye posteriorly just above the disc and diverge to run forwards in the choroid on its nasal and temporal sides to supply the choriocapillaris. From this layer blood is gathered into the central venous plexus of Gaupp, the flat vessels of which run in a general vertical direction in the midst of the choroid ; these converge to leave the globe—dorsally as two veins which unite to form the superior bulbar vein, ventrally as a single vein which enters the jugular vein. After giving off the ciliary branches the main trunk of the ophthalmic artery enters the globe on its under aspect in the region of the foetal fissure and runs forward to the ciliary region ; here, at the mid-ventral point, it sends off two branches which run circumferentially round the ciliary body as an arterial circle. From this the superficial arteries of the iris emerge ; the corresponding veins lie more deeply and drain partly into the venous plexus of the ciliary body and thence to the choroidal veins, partly through the two crescentic segments of the ciliary venous sinus into the subconjunctival vein. After it has given off the ciliary arterial circle, the ophthalmic artery turns backwards on itself as a "hyaloid artery" and almost immediately divides into two branches, a nasal and temporal, which

form an incomplete ring round the circumference of the ora ; thence branches run posteriorly to form a MEMBRANA VASCULOSA RETINÆ lying in the vitreous on the surface of the retina, a form of vascularization analogous to that seen in many Fishes¹ (Plate III : Figs. 405-6) (Hyrtl, 1861 ; Cuignet, 1866 ; Hirschberg, 1882). The capillaries of this system form a close net at the posterior pole but are few in the periphery and are associated with the veins rather than the arteries. They are collected by three large venous trunks, a ventral, a nasal and a temporal, and combine to form a hyaloid vein which eventually leaves the globe alongside the entering artery and drains into the ophthalmic vein. It is interesting that the arteries of the anterior segment are plentifully



FIG. 405.—INJECTED MEMBRANA VASCULOSA RETINÆ OF AN ADULT FROG. There is a capillary-free zone around the artery (A) (p. 161) (I. C. Michaelson).

provided with pad-like valves (Grynfeltt, 1907) while in the hyaloid vessels of the vascular membrane of the retina contractile cells are unusually prominent (Rouget, 1873 ; Mayer, 1902) ; it is possible, therefore, that there may be a switch-mechanism from one circulation to the other as illumination and activity vary.

Ophthalmoscopically the *retina* of the frog appears as a somewhat mottled slatey-grey background over which the semi-opaque nerve fibres radiate in immense numbers uniformly from the optic disc to the periphery in *Rana*, for a relatively short distance in *Bufo* and *Hyla* ; in these latter the remainder of the fundus is covered with orange or golden sago-like grains. In the Ranidae and Bufonidae the optic disc is long and narrow, resembling in its appearance a white caterpillar lying vertically ; in the Hylidae it is circular ; sometimes it is covered by a dark grey or even black pigment (the giant toad, *Bufo*



Bufo



Hyla

¹ p. 299.

marinus). The most prominent feature in the fundus is the vessels of the vascular membrane. These stand out clearly, and in the main vessels the large nucleated erythrocytes characteristic of Amphibians can be seen clearly as brilliantly-lit points racing along after each other. The arteries are thinner than the veins and lie over them; the veins are gathered into a large VENA MEDIA which stands out in conspicuous relief as it courses vertically downwards over or near the optic disc to disappear in the ventral area of the fundus (Cuignet, 1866; Hirschberg, 1882; Johnson, 1927) (Plate III).

The pigment epithelium of the retina is possessed of long processes dipping down among the visual elements.

The visual retina is avascular and has the usual vertebrate architecture, the layers being of average thickness (Figs. 406-7). The visual cells, however, are of unusual interest and have received much study (Figs. 408-9).¹ They are commonly of four types, all of them large and coarse in structure: violet and green rods, single cones and double visual elements, while triple visual elements have been described. The violet (or red) rod, which contains rhodopsin, is unusually plump, the outer segment unusually large and the nucleus in contact with the external limiting membrane, a level generally occupied by the nuclei of cones. The green rod (of Schwalbe) is found only in Amphibians among which, however, it is widely distributed (Denton and Pirenne, 1952); it has a smaller outer segment lacking rhodopsin, a long slim stalk, and its nucleus lies at a deeper level in the inner part of the outer nuclear layer; in structure it therefore occupies an intermediate position between a cone and an ordinary (red) rod (Walls, 1942). The single cones resemble those of the Holosteans and Dipnoi, and in diurnal types (*Rana*) they possess a yellow oil-droplet in the upper part of the ellipsoid, a structure first described by H. Müller (1861) and Babuchin (1863-64). Double visual elements commonly occur, usually said to be "double cones" but perhaps representing the fusion of a rod and cone (Saxén, 1954-56); in these the oil-droplets are confined to the main member of the pair. Triple cones, only two members of which bear oil-droplets, have been described by Saxén (1953) in the retina of *Rana temporaria*, a formation suggesting that these and the double cones result from a fusion of elements rather than from a process of cell-division. There is a vague area centralis which has probably more resolving power than the remainder of the retina (Krause, 1875); it



Rana

¹ H. Müller, 1857; Hulke, 1864; Schultze, 1866; Steinlin, 1868; Dobrowolsky, 1871; Landolt, 1871; Schwalbe, 1874-87; Krause, 1875-92; Hoffmann, 1876-77; Boll, 1877; Kühne, 1878; Dogiel, 1888; Cajal, 1893; Greeff, 1899; Gaupp, 1904; Kolmer, 1904; Hesse, 1904; Garten, 1907; Hess, 1910; Arey, 1916; Majima, 1925; Noble, 1931; Rozemeyer and Stolte, 1930; Police, 1932; Detwiler, 1943; Bau-van-Kien, 1954; and many others. For ultramicroscopic structure, see Sherman, 1954; for localization of mitochondria, see Carasso, 1954; for histochemistry, see Sasaki and Sidman, 1954; for development, see Saxén, 1954-56.

PLATE III
THE EYES OF ANURANS

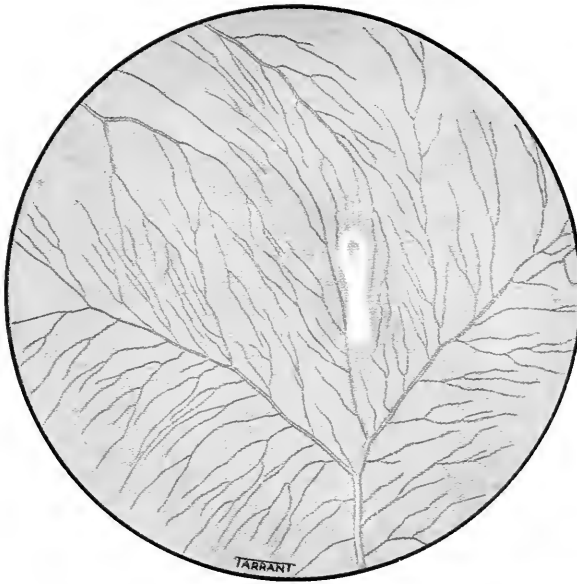


FIG. 1. —The fundus of the frog, *Rana temporaria*.

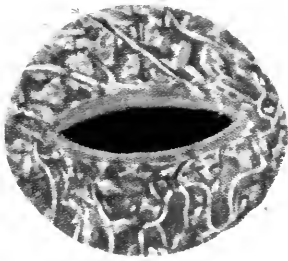


FIG. 2. —The iris of the giant toad, *Bufo marinus* (blood flow shown by arrows) (Ida Mann).



FIG. 3. —The iris of the common frog, *Rana temporaria* (Ida Mann).

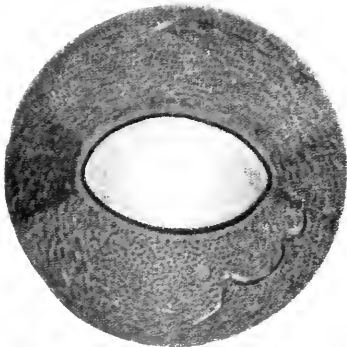


FIG. 4. —The iris of the Malayan tree-frog, *Rhacophorus leucomystax* (Ida Mann).



FIG. 5. —The iris of White's tree-frog, *Hyala carulea* (Ida Mann).

FIGS. 406 AND 407.—THE ANURAN RETINA.

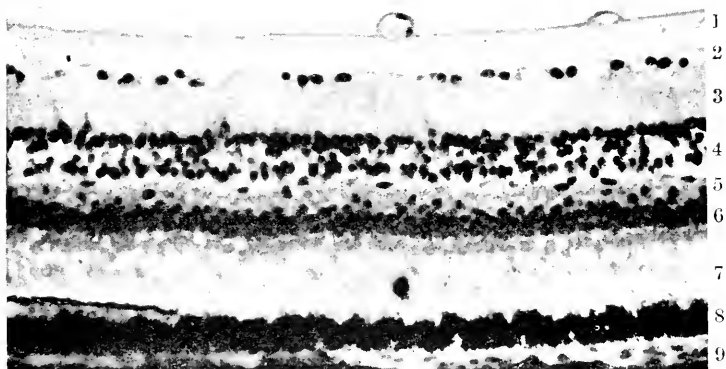


FIG. 406.—The retina of *Rana temporaria*.

Note the vessels of the membrana vasculosa retinae lying on the inner surface of the retina (above) ($\times 320$) (Norman Ashton).

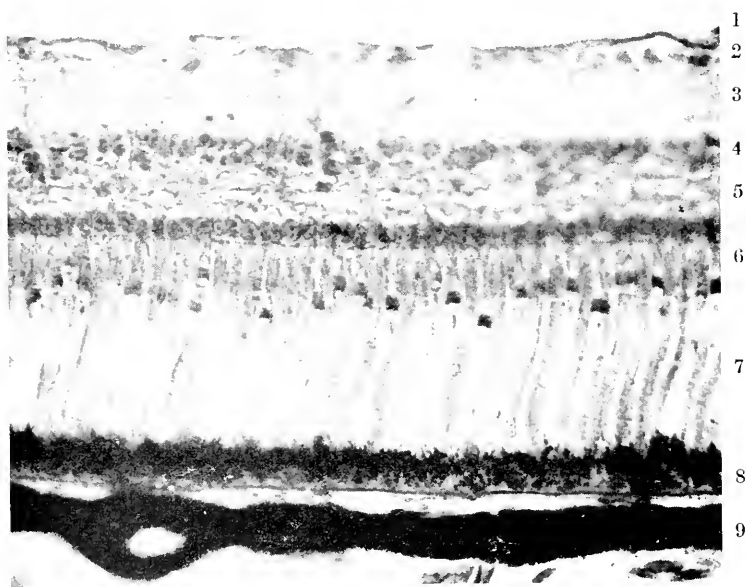


FIG. 407.—The retina of *Xenopus laevis* ($\times 450$) (Katharine Tansley).

(1) optic nerve fibre layer ; (2) ganglion cells ; (3) inner plexiform layer ; (4) inner nuclear layer ; (5) outer plexiform layer ; (6) outer nuclear layer ; (7) visual cells ; (8) pigmentary epithelium ; (9) choroid.

assumes varying shapes—a crescent above the optic disc in *Rana*, a circle around it in *Hyla* and *Bufo*, a linear band in *R. esculenta*, and so on (Hulke, 1864 ; Chievitz, 1891 ; Slonaker, 1897 ; von Hess, 1910).

The *optic nerve* is thin and cylindrical with connective tissue septa

FIGS. 408 AND 409.—THE VISUAL CELLS OF ANURANS.

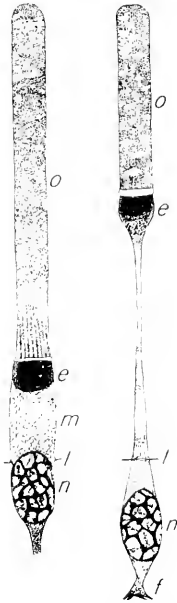


FIG. 408.—The dark-adapted common rod (on the left) and the green (Schwalbe's) rod of the leopard frog, *Rana pipiens* (on the right) (Gordon Walls).

e, ellipsoid ; *f*, foot-piece ; *l*, ext. limiting membrane ; *m*, myoid ; *n*, nucleus ; *o*, outer segment.

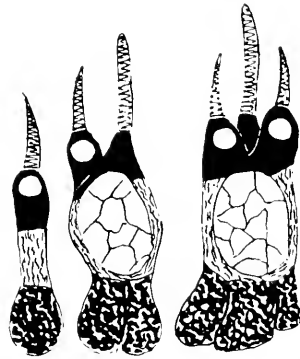


FIG. 409.—Single, double and triple cones from the eye of the tadpole of *Rana temporaria* (aged 26 days).

There is an achromatic oil-droplet in the single cone, in the chief member of the double cone, and not in the accessory member of the triple cone. In the double cones the accessory member has an extensive paraboloid and a rod-shaped outer segment. In the triple cone there are 3 components, 2 similar in all respects to the chief component of the double cone, the third similar to the accessory element of the double cone (L. Saxén).

(Studnicka, 1898), while the chiasma shows a total decussation frequently in the form of large fasciculæ interdigitating with one another (J. Müller, 1826 ; Leuckart, 1876 ; Gross, 1903).

THE OCULAR ADNEXA are very different from those of Fishes, for in the result a complicated protective and lubricating system is necessary to protect an eye exposed to air ; *lids* are thus absent in the larvæ of

Amphibians, all of which are aquatic, and in those adult frogs which do not leave the water. In the majority, however, which live their adult life on land, a short upper and lower lid develop during metamorphosis (Maggiore, 1912); the upper lid is immobile, but associated with the lower an elastic translucent fold forms a *false nictitating membrane*, the free border of which is usually spotted with a brilliant bronze pigment (green in some Hylidae, as *Hyla carulea*). Normally the lid lies as a Z-shaped fold in the lower fornix and its thickened upper border is continued as a cord which runs around the posterior part of the eyeball slinging itself around the retractor bulbi muscle (Fig. 410): when this muscle contracts the eye is pulled into the orbit and the tug on the cord draws the membrane upwards over the cornea completely covering it. The membrane is thus entirely passive in its action and, forming part of the lower lid itself, differs fundamentally from the pseudo-nictitating membrane seen in some Teleosteans and also from the true nictitating membrane of the higher Vertebrates. Lubrication is effected by a development of glands in the margin of the upper lid: those on the nasal side hypertrophy to form the massive harderian gland¹ which occupies a considerable space in the nasal half of the orbit, while those on the temporal side become the precursor of the lacrimal gland: two puncta appear on the free border of the lower lid, the canaliculi uniting into a subcutaneous naso-lacrimal duct running horizontally into the middle fossa of the nose.

Ocular movements, apart from retraction, are negligible. The usual 6 extra-ocular muscles, however, are present with, in addition, a powerful RETRACTOR BULBI MUSCLE innervated by the VIth nerve and probably derived from the external rectus, and a second muscle behind the eye, the LEVATOR BULBI, derived from the jaw-musculature and supplied by the Vth nerve. If the eye is touched, retraction of the globe is effected by the retractor muscle which at the same time pulls the nictitating membrane over the cornea: thereafter the levator bulbi pulls the globe forward again and the membrane of the lower lid falls back into its normal folded position. This movement of retraction, however, is possibly as useful as an aid to swallowing food as a protective device: the partition between the orbit and the mouth is merely a thin membranous sheet and when the eyeball is pulled into the head

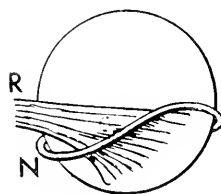


FIG. 410.—MUSCULATURE OF THE NICTITATING MEMBRANE OF THE FROG.

R, retractor bulbi muscle; N, tendon of nictitating membrane on the temporal side of the posterior aspect of the globe (after Franz).

¹ In most Vertebrates the lids are lubricated by a row of compound glands which are frequently best developed temporally and nasally: those on the temporal side develop into the LACRIMAL GLANDS secreting tears, those on the nasal side into the GLAND OF HARDER (*Acta eruditiorum pub.*, Lipsiae, 1694) with a sebaceous oily secretion.

it bulges downwards into the roof of the mouth, thus forcing food down the throat.

The anuran *orbit* is large and membranous with considerable gaps in its walls and without an interorbital septum or any division between the two cavities. As we have seen, the orbital cavity opens directly into the pharynx.

THE URODELAN EYE

MANY OF THE TAILED AMPHIBIANS, with their cavernicolous and secretive habits, have reduced or degenerate eyes¹; even those types which are visually active, such as the salamanders and newts (*Salamandra*, *Triturus*) and Axolotl (the larva of the salamander, *Ambystoma tigrinum*), have eyes which are smaller and simpler than those of Anurans although designed on the general amphibian plan (see Okajima, 1909; Rochon-Duvigneaud, 1943). The main differences are the



Ambystoma



FIG. 411.—THE HEAD OF THE NEWT, *TRITURUS*.



FIG. 412.—THE AXOLOTL, LARVA OF *AMBYSTOMA TIGRINUM* (Zool. Soc., London).

¹ p. 726.

PLATE IV
THE EYES OF URODELES

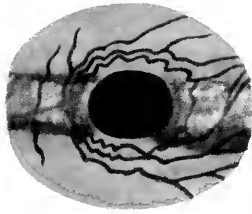


FIG. 1.—The iris of the Californian newt, *Triturus torosus* (Ida Mann).



FIG. 2.—The fundus of *Salamandra maculosa*
(Lindsay Johnson).

fibrous sclera without cartilage (except for anterior cartilaginous plaques in *Triton*, and the small fragmented cartilage in *Hynobius*—Stadtmüller, 1914–29 ; Tsusaki, 1925 ; Inagaki, 1930 ; Yatabe, 1931), the comparatively large size of the lens as would be expected in creatures favouring dimly-lit surroundings, the comparatively shallow anterior chamber, the thicker and less highly organized choroid separated from the sclera by large serous spaces, the lack of ciliary folds on the inner surface of the ciliary body and iris with the exception of a single mid-ventral ciliary process, the lack of a dorsal protractor lentis muscle in the place of which the suspensory ligament is strengthened locally as in Fishes, the lack of pupillary nodules, of the primitive and discontinuous ciliary venous sinuses, and of an area centralis in the retina. Accommodation is thus effected through a ventral protractor lentis muscle after the manner seen in selachian fishes, by a forward pendular movement of the lens rather than its forward displacement as a whole (Beer, 1898).

The vascular supply to the anterior segment is similar in its general plan to that of the Anurans, but curiously the vascular arrangements in the iris partake of a more definite pattern (Plate IV) : as in the frog, the arteries are superficial but instead of entering at various apparently haphazard positions around the circumference as in this animal, they are represented in the salamander by two trunks, an inferior and a temporal artery of the iris, an arrangement anticipating that seen typically in Reptiles such as the lizard (Plate V) (Mann, 1929). Sometimes the inferior artery of the iris is a branch of the temporal and does not enter separately. The arteries break up irregularly round the pupil and the blood is drained away by a few radial veins lying in a deeper plane so that they are often obscured by pigment. In newts (*Triturus*, *Pleurodeles*) the artery breaks up into some 6 branches which encircle the pupil and drain away on the nasal side (Mann, 1931).

In tailed Amphibians the pupil is usually round and the iris may be brilliantly pigmented—dark brown with faint metallic flecks in the spotted salamander (*Salamandra maculosa*), horizontal green and brown banding in the Californian newt (*Triturus torosus*), sage-green with peripheral horizontal bands of metallic gold in the Japanese newt (*Triturus pyrrhogaster*), and so on (Mann, 1931) (Plate IV, Fig. 1).

The fundus in salamanders is uniformly the same throughout, of a pinkish hue with a granular texture in the middle of which the circular grey optic disc is set (Plate IV, Fig. 2). The retina is avascular and there is no membrana vasculosa retinae as in Anurans (Virchow, 1881) (*Salamandra*, Hyrtl, 1861 ; *Triton*, Kessler, 1877).

The visual elements tend to be sparser and larger than in the frog, but are generally of the same morphological types except for the absence of oil-droplets in the cones (Fig. 413–5), and the occasional lack of green rods (in *Salamandra*).



Triturus cristatus
(male)



Triturus cristatus
(female)

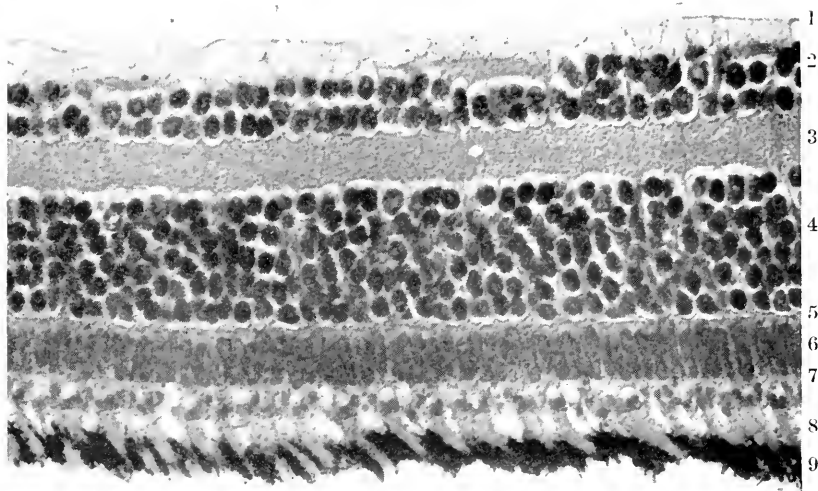


FIG. 413.—THE RETINA OF THE NEWT, *TRITURUS*.

1, optic nerve fibres; 2, ganglion cells; 3, inner plexiform layer; 4, inner nuclear layer; 5, outer plexiform layer; 6, outer nuclear layer, consisting of large elongated nuclei; 7, external limiting membrane; 8, visual cells; 9, pigment ($\times 253$) (Katharine Tansley).

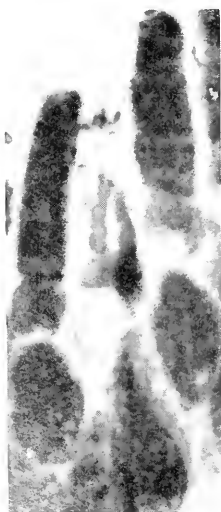


FIG. 414.—A DOUBLE CONE IN THE EYE OF A NEWT (Azari; 1929) (Katharine Tansley).

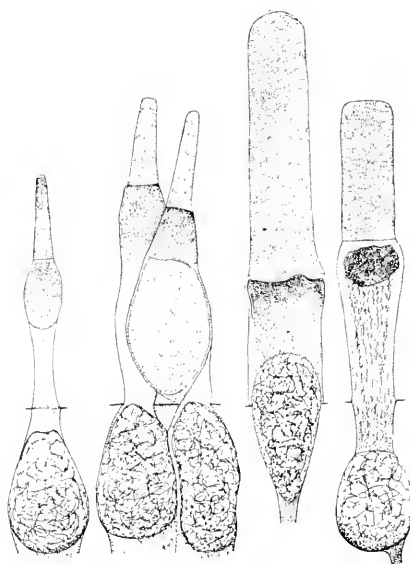


FIG. 415.—THE VISUAL CELLS OF THE AXOLOTL, *AMBYSTOMA TIGRINUM*.

A single cone, a double cone (compare Fig. 414), a common rod and a green (Schwalbe's) rod ($\times 1,000$) (Gordon Walls).

Movable eyelids are found only in the Urodeles which have adopted terrestrial life; in aquatic forms the lids have receded to immovable ridges or low folds, while in subterranean species the eyes are completely covered by the skin.¹ It is interesting that in terrestrial salamanders the lacrimal glands are distributed along the lower lids (Piersol, 1887; Maggiore, 1912; Engelhardt, 1924).

The limicoline types of the Urodela which live in mud, such as the North American genera, *Cryptobranchus*, *Amphiuma*, *Necturus* and *Siren*, have relatively



Megalobatrachus



Amphiuma

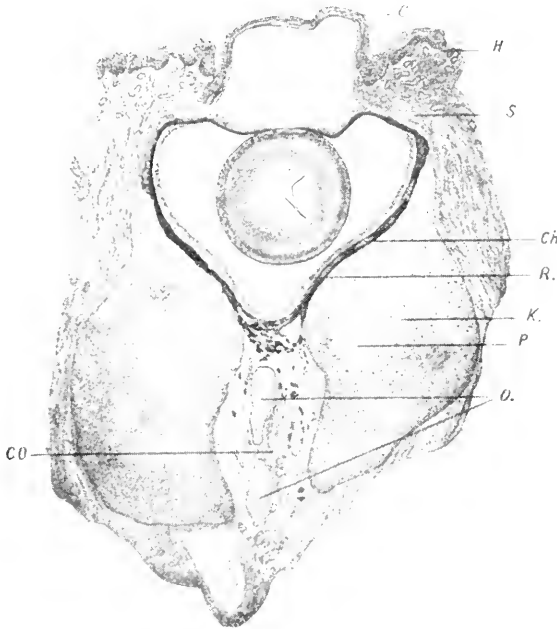


FIG. 416.—THE EYE OF *MEGALOBATRACHUS MAXIMUS*.

A section of the ill-formed eye of this Urodele. *C*, cornea; *Ch*, choroid; *CO*, optic canal; *H*, skin; *K*, the enormously large scleral cartilage with its dense core; *P*; *O*, optic nerve; *R*, retina; *S*, fibrous tissue of sclera (after Lauber).

crude and ill-developed eyes which seem incapable of elaborate optical imagery. In the related Japanese giant salamander, *Megalobatrachus maximus*, found also in China and Tibet — incidentally the largest extant Amphibian, 5 feet in length — the monstrously hypertrophied scleral cartilage occupies more space than the remainder of the eye; indeed, this cartilage is the most massive seen among the Vertebrates and occupies two-thirds of the section of the globe (Lauber, 1902; Reese, 1905; Yano, 1926–28; Aoyama, 1928; Stadtmüller, 1929) (Fig. 416). In this salamander also, as in some other Japanese types, the cornea is vascularized (Tawara, 1933; Kurose, 1956). The visual elements are similarly sparse



Necturus

¹ p. 726.

and crude. The violet rods of the mud-puppy, *Necturus*, for example, are enormous, two and a half times the thickness of the corresponding structures in the frog and the largest known in the vertebrate phylum. The optic nerve fibres are relatively few, one ganglion cell subserving more visual elements than in the frog (Burkhardt, 1931). Thus there are, according to Palmer's (1912) heroic counting, only 962 nerve fibres subserving the 53,000 rods, 42,000 single cones and 15,000 double cones in the retina.

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FIG. 417.—GORDON L. WALLS (1905—).

CHAPTER XIII

THE EYES OF REPTILES

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

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

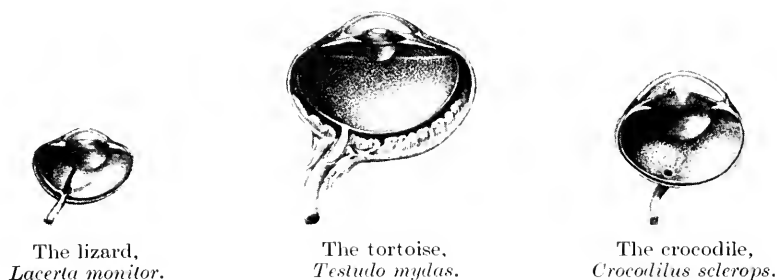
We shall therefore describe the eyes of lizards in some detail as the essential reptilian type, enumerate shortly the main simplifications seen in the first three groups, and finally discuss the unique eyes of snakes.

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

THE EYE IN EVOLUTION

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

FIG. 418.—THE EYES OF REPTILES.



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

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

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

A striated iris musculature giving the iris considerable mobility.

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

A pattern of iris vascularization consisting of deep circumferential

arteries and superficial radial veins in place of the reverse arrangement in *Ichthyopsida*.

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

THE LACERTILIAN EYE

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

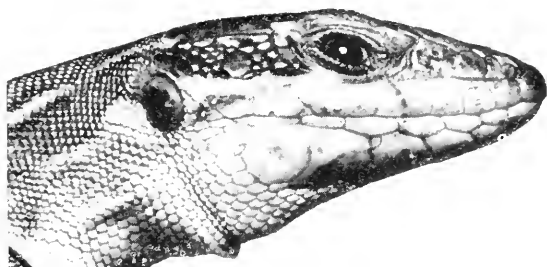


FIG. 419.—THE HEAD OF THE LIZARD, *LACERTA MURALIS* ($\times 3.5$) (Katharine Tansley).



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

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

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



Chlamydosaurus

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

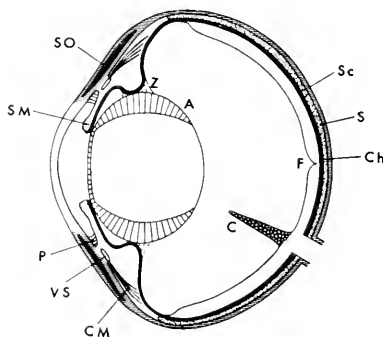


FIG. 421.—DIAGRAM OF THE EYE OF A LIZARD.

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

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



Gecko

The *uvea* in general is thin. The *choroid* forms a tenuous layer without distinctive characteristics. The *ciliary body* varies in shape—narrow and angular in the geckos, broad and rounded in the chameleon—and has no ciliary processes but abuts directly on the annular pad

of the lens (Figs. 423-4). The musculature is complicated and is divided into 3 systems. The ciliary muscle (of Brücke) is well developed, the fibres running meridionally from their origin from the inner layers of the cornea, not to the choroid as does the tensor choroideae of Fishes and Amphibians (or the ciliary muscle of Mammals), but to the orbiculus ciliaris, where its anchorage is continued by a TENACULAR LIGAMENT running from the orbiculus into the sclera. These fibres are particularly marked anteriorly, those arising from the cornea being to some extent isolated to form the MUSCLE OF CRAMPTON, a muscular bundle more fully developed in Birds.¹ The meridional ciliary fibres are sometimes augmented by circumferential fibres arising dorsally and extending round in the temporal half of the globe; and in most species by an inferior TRANSVERSE MUSCLE. This muscle arises ventrally from the connective tissue between the ciliary body and the sclera and passes through an open portion of the foetal cleft to be inserted into the zonular fibres and thus indirectly to the lens. It would seem analogous to the protractor lentis muscle of Amphibians and probably moves the lens nasally during accommodation, presumably to increase convergence (*Seps*, *Lacerta*—Leplat, 1921).

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

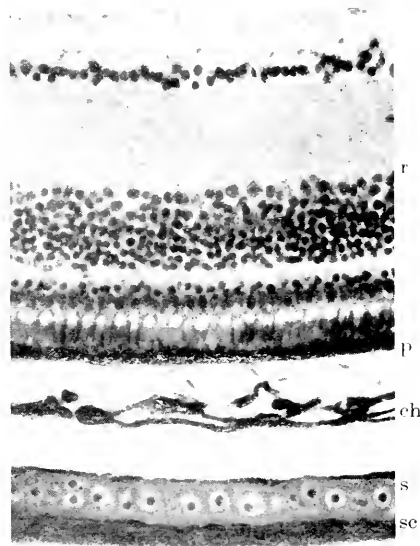
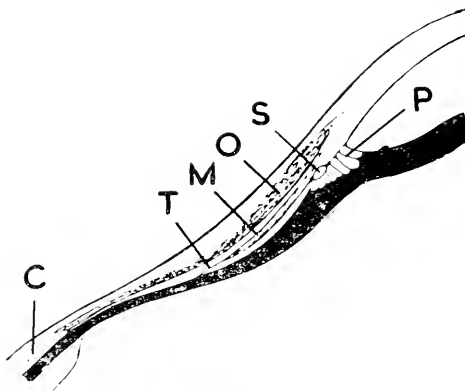


FIG. 422.—THE POSTERIOR SEGMENT OF THE EYE OF THE LIZARD.

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

¹ p. 405.

FIGS. 423 AND 424.—THE CILIARY REGION OF THE LACERTILIAN EYE.

FIG. 423.—The lizard, *Tupinambis*.

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

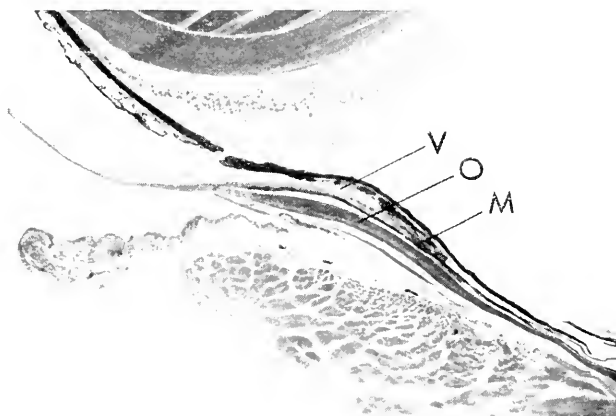


FIG. 424.—The skink.

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

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

*Iguana tuberculata*

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

PLATE V
THE IRIDES OF LIZARDS
(Ida Mann)

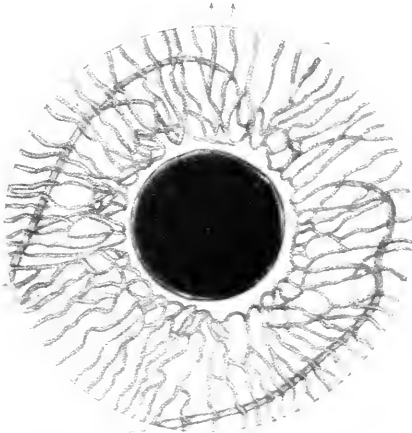


FIG. 1.—Cochin-China water-lizard, *Physignathus cochinchinensis* (right eye).



FIG. 2.—Agamid lizard, *Agama agama*.

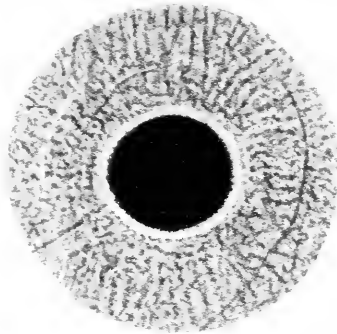


FIG. 3.—Yrpha iguana, *Ophryotrocta superciliosa*.

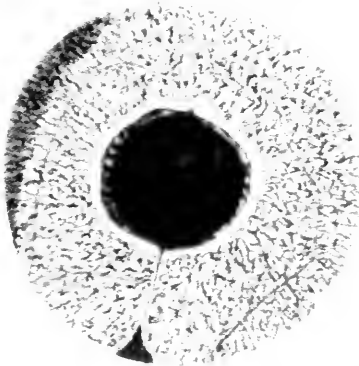


FIG. 4.—African plated lizard, *Gerrhosaurus granulatus*.

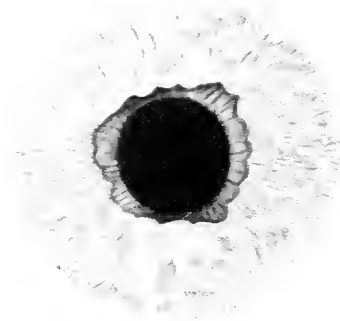


FIG. 5.—Black-pointed teju, *Tupinambis nigropunctatus*.

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

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



Agama

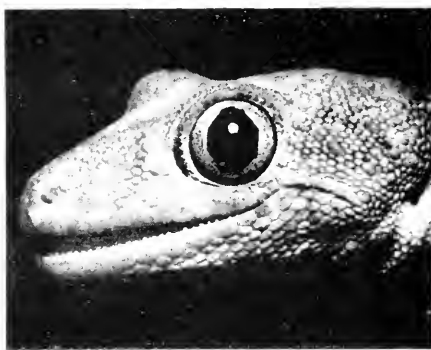
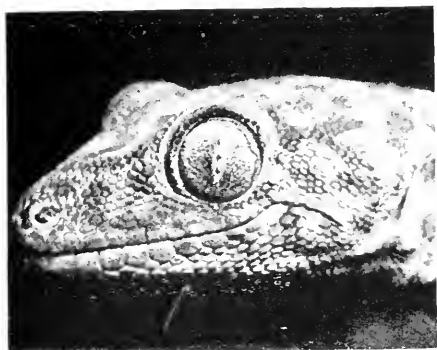


FIG. 425.—THE PUPILS OF A NOCTURNAL GECKO.

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

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

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



Heloderma

¹ Analogous to the canal of Schlemm.

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



FIG. 426.—Section through the amular pad of the skin. The iris and cornea above and to the right ($\times 70$) (Norman Ashton).

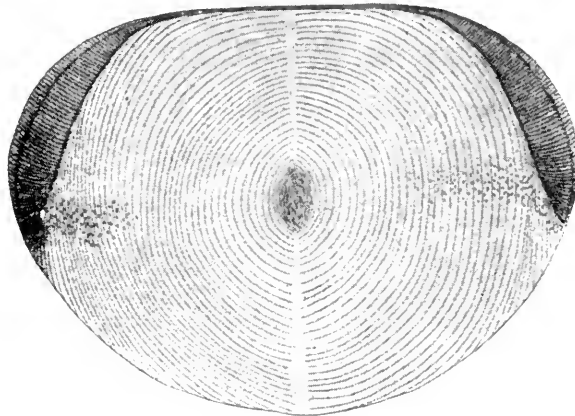


FIG. 427.—The lens of *Lacerta*, showing a small annular pad (after Rabl).

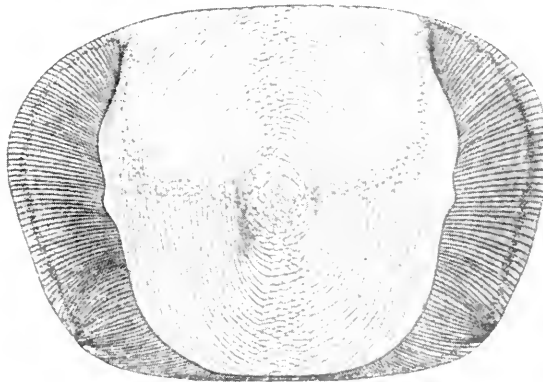


FIG. 428.—The lens of the chameleon. Showing a large annular pad (after Rabl).

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

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

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

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



Anolis

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

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

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

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

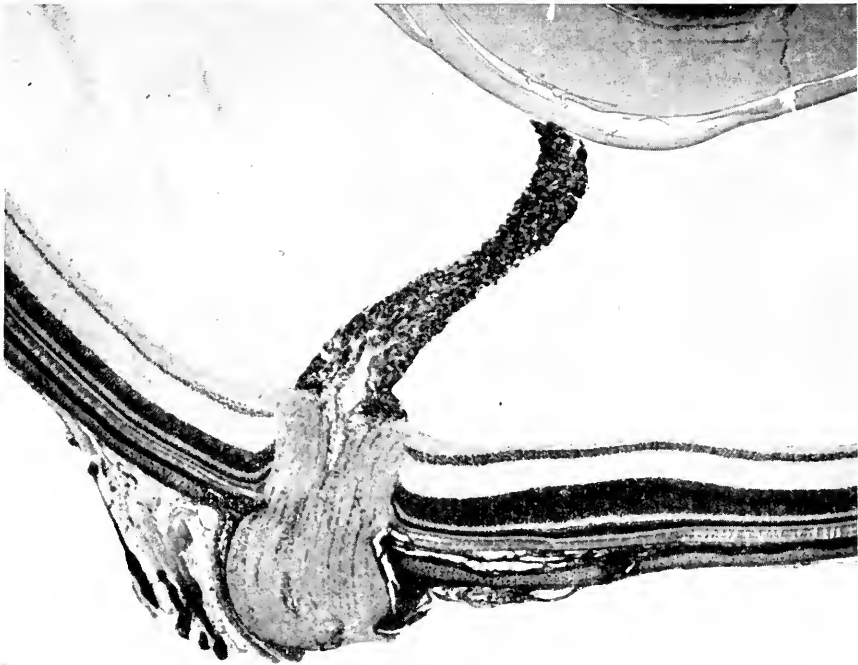


FIG. 429.—THE POSTERIOR POLE OF THE EYE OF THE LIZARD, *LACERTA MURALIS*.
Showing the optic nerve and the conus papillaris approaching the lens ($\times 50$)
(Katharine Tansley).

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

¹ (1853), Hulke (1864), H. Müller (1862), Beauregard (1876), Kopsch (1892), and others. (1901), Jökl (1923), Johnson (1927), and many others.

PLATE VI
THE FUNDI OF LIZARDS
(Lindsay Johnson)

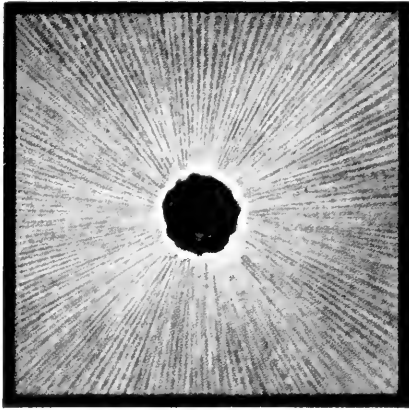


FIG. 1.—Alligator lizard, *Anolis alligator*.



FIG. 2.—Turkish gecko, *Hemidactylus turcicus*.



FIG. 3.—Galapagoan iguanid, *Conolophus subcristatus*.



FIG. 4.—Black iguana, *Metopoceros cornutus*.

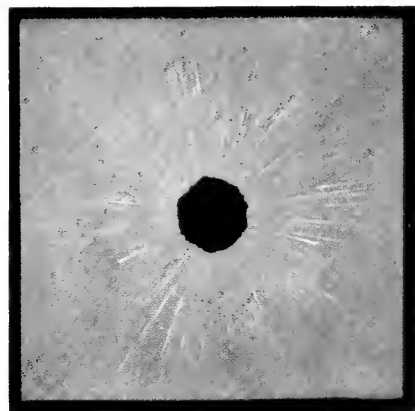


FIG. 5.—Chameleon, *Chamaeleon vulgaris*.

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

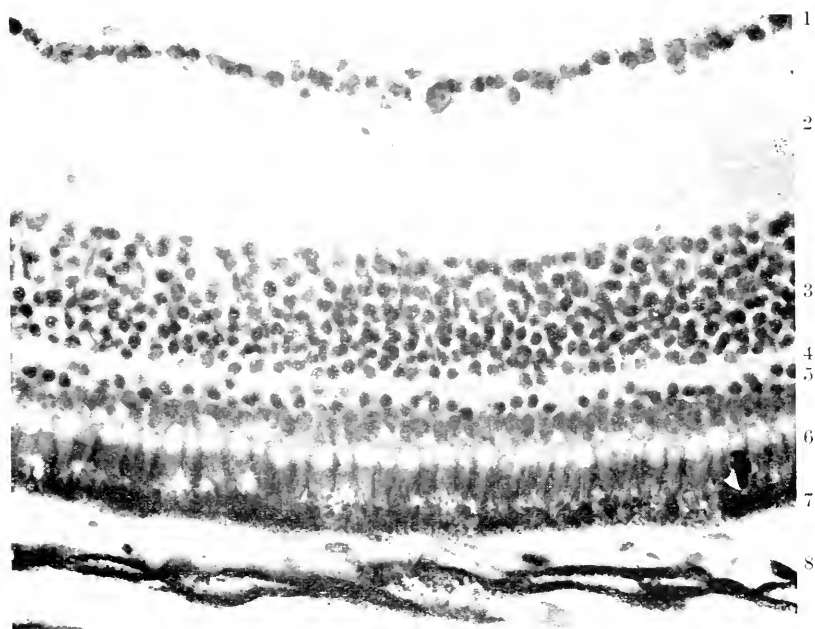


FIG. 430.—THE RETINA OF THE LIZARD.

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

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

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



Anguis

¹ p. 733.

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

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

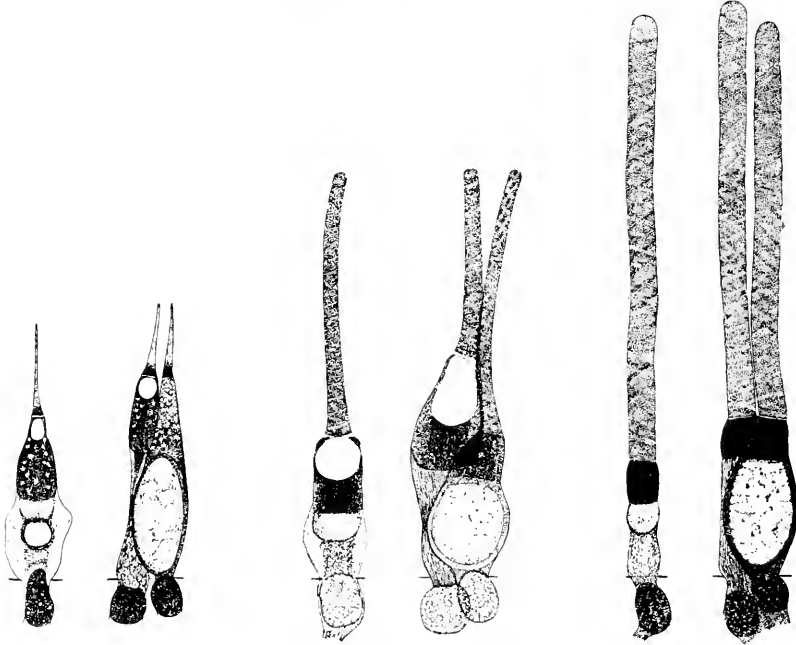


FIG. 431.—The cones of a diurnal lizard, *Crotaphytus*.

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

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

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

¹ Aristelliger Underwood noted occasional triple visual cells.

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



Phrynosoma

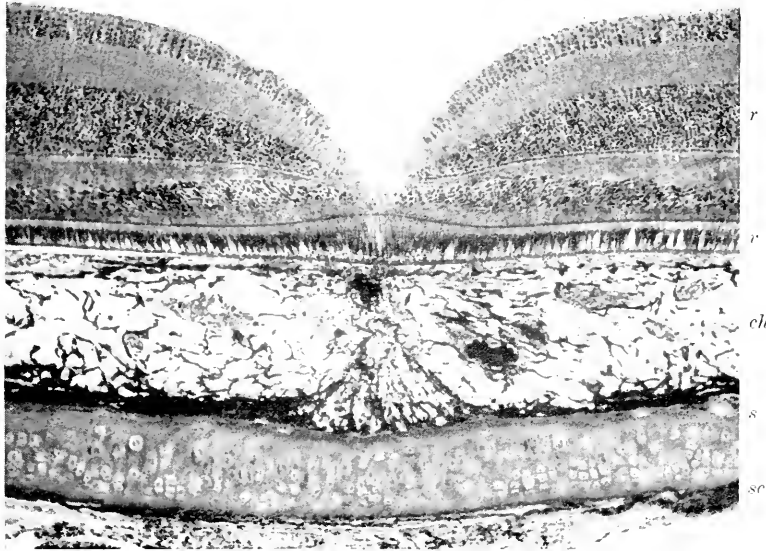


FIG. 434.—THE REMARKABLY WELL-FORMED FOVEA OF THE GIPPSLAND WATER-DRAGON, *Phrynosoma* (O'Day).

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

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

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

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

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



Chameleon

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



Skink

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

¹ p. 694.

² Only in some Mammals (the leopard, bat and hedgehog) is cartilage found in the tarsal plate.

³ p. 266.

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

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

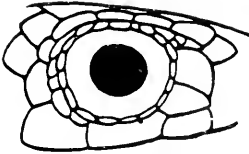


FIG. 435.—*Ablepharus*.

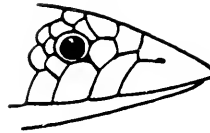


FIG. 436.—*Typhlaontias*.

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

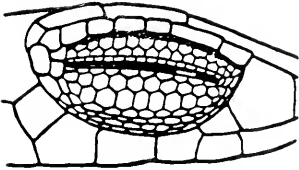


FIG. 437.—*Zonosaurus*.

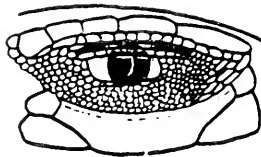


FIG. 438.—*Eremias*.

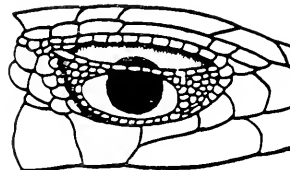


FIG. 439.—*Mabuya*.

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



FIG. 440.—*Anolis lucius*.



FIG. 441.—*Anolis argenteolus*.

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

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

When the lower lid is mobile and opaque, a transparent nictitating membrane is formed from a vertical fold of the conjunctiva at the nasal corner of the palpebral aperture which can be swept across the cornea from the nasal to the temporal side. Moisture and lubrication are usually attained by a lacrimal gland with several contractile ducts at the temporal canthus and a large harderian gland

lying naso-ventrally provided with a single duct (Loewenthal, 1935-36 ; Schwarz-Karsten, 1937 ; Bellairs and Boyd, 1947-50). The lacrimal gland, however, is absent in the chameleon and many geckos. The naso-lacrimal duct enters the nose within the accessory olfactory vomero-nasal organ of Jacobson. The nictitating membrane is pulled across by a tendon-like cord arising from its free edge and attached to the dorsal wall of the orbit, its movements being controlled by a special arrangement of muscles behind the eyeball (Fig. 442).

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



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

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

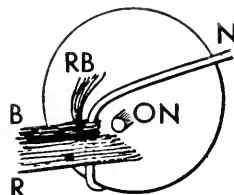


FIG. 443.—THE POSTERIOR ASPECT OF THE GLOBE OF *LACERTA*.

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

optic nerve and round it the tendon of the nictitating membrane loops so that the latter is drawn taut when the muscle contracts ; from it a muscular slip runs upwards to be inserted more dorsally in the sclera, the RETRACTOR BURSALIS, which acts by bracing the bursalis so that the muscular apparatus and the looped tendon are kept away from the optic nerve when contraction occurs. In most lizards ocular movements are sluggish or occasionally absent, a marked and extraordinary exception being the insectivorous chameleon¹ : in it the extra-ocular muscles are very fully developed (Leblanc, 1925).

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

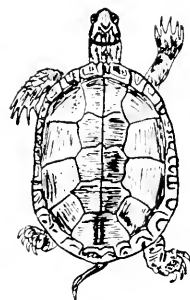
THE CHELONIAN EYE

THE TORTOISES AND TURTLES are the most ancient of surviving Reptiles²—sluggish animals encased in a dorsal and ventral bony carapace, the shelter of which the head as well as the limbs and tail can

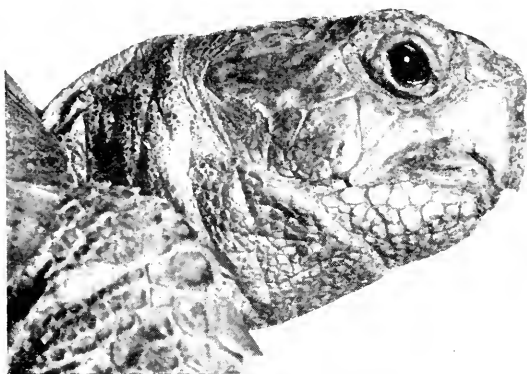
¹ p. 694.

² p. 234.

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



Turtle

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

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

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

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

FIGS. 445 AND 446.—THE CHELONIAN EYE.

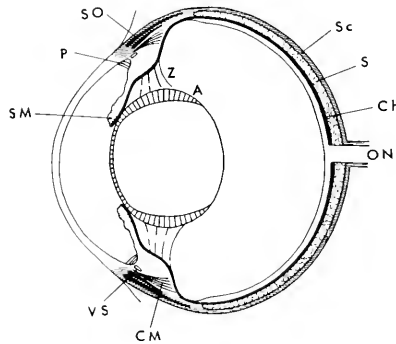
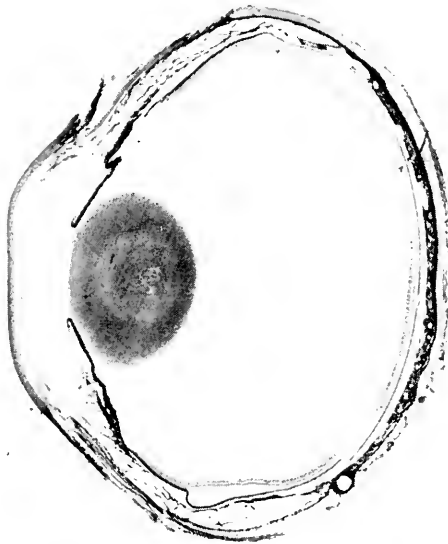


FIG. 445.—Diagram of a Chelonian eye.

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

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

leathery-skinned turtle, *Dermochelys*, Rochon-Duvigneaud, 1943) (Fig. 447). In aquatic forms, the iris has the same bright and variegated colour as in the lizard—red, yellow, green and brown—and in some species is striped in such a way that the pattern on the skin is continued over the iris as if for the purposes of camouflage (the terrapin, *Clemmys*, Mann, 1931 ; and particularly the painted turtle, *Chrysemys*.

Walls, 1942) (Plate VII).¹ In the land tortoises the colours are less bright, brown predominating. The common box tortoise, *Testudo carolina*, is peculiar in that it shows a remarkable instance of sexual dimorphism, the iris of the male being red, of the female brown.

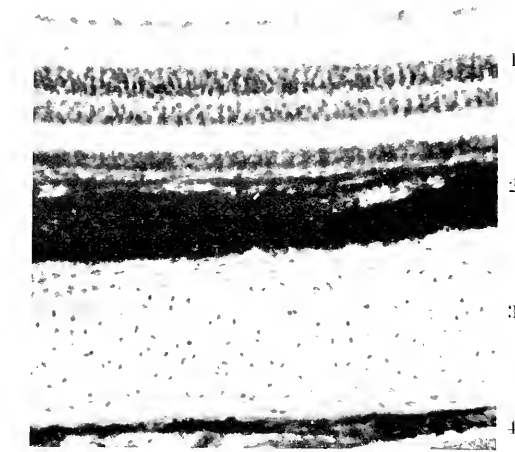


FIG. 447.—THE POSTERIOR SEGMENT OF THE EYE OF THE TORTOISE.
1, the retina : 2, choroid : 3, scleral cartilage : 4, fibrous sclera ($\times 112$)
(Katharine Tansley).



FIG. 448.—THE CILIARY REGION OF THE EYE OF THE TORTOISE.

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

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

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



Tortoise

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

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

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

Histologically the retina does not reach the high degree of definition in its architecture found in the lizard ; throughout its extent the different layers are by no means exclusively segregated but their elements tend to be intermingled (Figs. 449-452).¹ In the early stages of development an avascular glial cone may appear on the optic disc in some turtles² but this always disappears in the adult ; the retina is thus entirely avascular depending only on the choroid for its nourishment. The visual cells show a vast predominance of cones, either single or double, the former and one element of the latter containing an oil-droplet, orange, yellow or ruby-red in colour. Cells with a cone-like structure but resembling rods in the heaviness of the outer segment

¹ See Hulke (1864), Heinemann (1877), Chievitz (1889), W. Krause (1893), Pütter (1902).

² In the sea-turtle, *Chelonia*, the snapping turtle, *Chelydra*, the painted turtle, *Pseudemys*, etc.

PLATE VII

THE EYES OF CHELONIANS

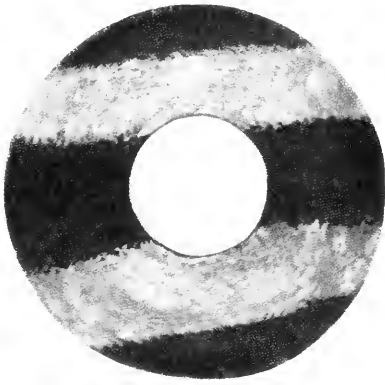


FIG. 1.—The iris of the painted turtle, *Chrysemys picta* (Ida Mann).

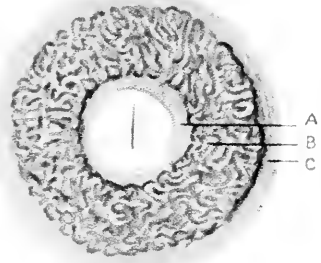


FIG. 2.—The iris of the European pond-tortoise, *Emys orbicularis*. A, thin circumpupillary zone; B, capillary plexus; C, zone of large vessels hidden by pigment (Ida Mann).

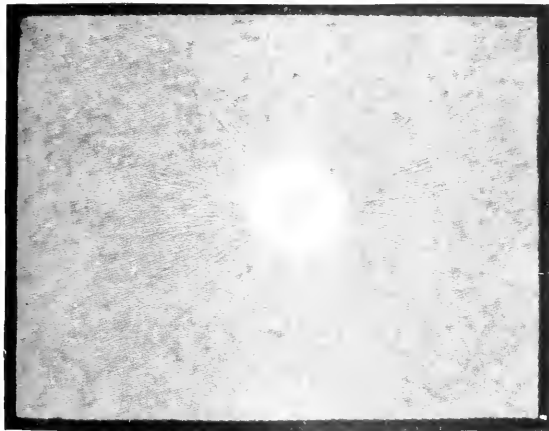


FIG. 3.—The fundus of *Cinysis crocei* (Lindsay Johnson).

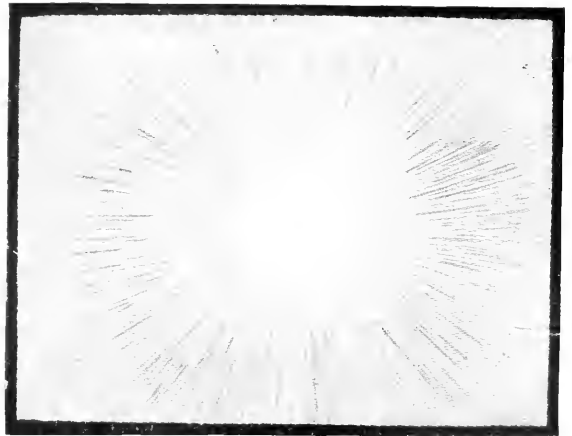


FIG. 4.—The fundus of the Burgoma river turtle, *Emys granosa* (Lindsay Johnson).

FIGS. 449 TO 451.—THE CHELONIAN RETINA.

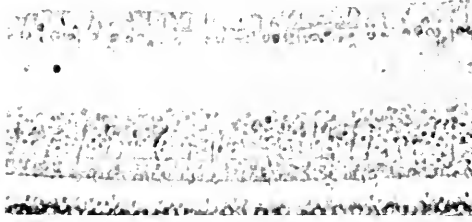


FIG. 449.—The retina of the tortoise ($\times 200$) (Norman Ashton).

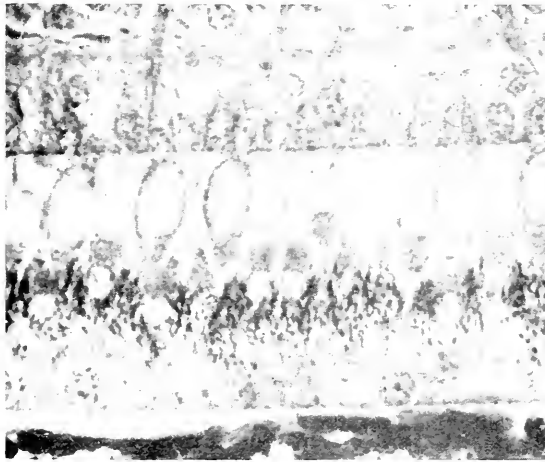


FIG. 450.—The visual cells of the tortoise ($\times 834$) (Norman Ashton).

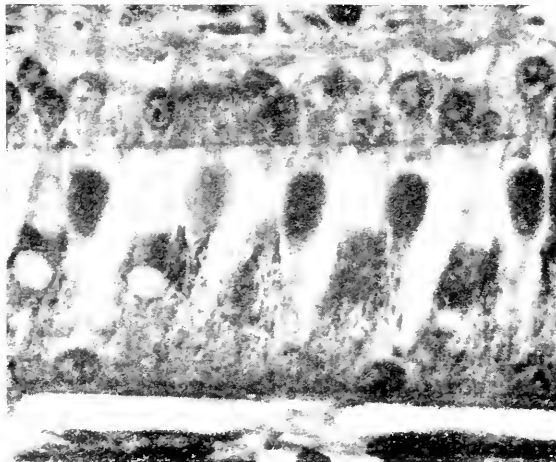


FIG. 451.—The visual cells of the Murray turtle, *Chelodina* (O'Day).

and the absence of an oil-droplet are also present ; these anomalous cells occur particularly in those species which habitually avoid the light (the snapping turtle, *Chelydra*) or are frankly nocturnal (the terrapin, *Pseudemys*) (Detwiler, 1916-43 ; Walls, 1934-42). The cones retract slightly on exposure to light (Detwiler, 1916) and, as in lizards, the migration of the retinal pigment is restricted (3.6μ in the tortoise, Detwiler, 1916).

An area centralis on the visual axis is present in the retina of most species where the cones are smaller and more densely packed than elsewhere and the increased number of nuclei determine a thickening of the nuclear layers¹ ; a fovea, however, is absent except as a rarity when a shallow depression is found.² In the central area the ratio of receptor cells to ganglion cells is 1 : 1, while in the periphery it is 3 : 1.³

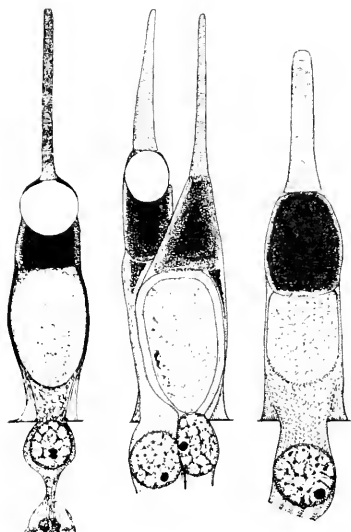


FIG. 452.—THE VISUAL CELLS OF THE SNAPPING TURTLE, *CHELYDRA*.

A single cone, a double cone and a rod ($\times 1,000$) (Gordon Walls).



Terrapin

THE OCULAR ADNEXA. Of the two lids the lower is the larger and more mobile and the palpebral aperture, horizontal in the lacertilian eye, is canted so that it runs from the dorso-temporal to the ventro-nasal quadrants of the eye, as if to make it parallel with the surface of the water in aquatic types when swimming with the head raised above the surface. Only rarely is there a transparent window in the centre of

the mobile lower lid (the Murray turtle, *Chelodina* ; the turtle, *Emyda*). The movements of the lower lid and the semi-opaque nictitating membrane are controlled by two long tendons which arise from a fan-shaped PYRAMIDALIS MUSCLE fixed to the posterior aspect of the globe (Fig. 453) ; the retractor bulbi muscle is powerful and when it contracts the globe is drawn inwards and twisted far round, the lower lid and nictitating membrane covering the eye at the same time. So forceful may this movement be in some turtles that when the lower lid closes against the upper the action is continued so that the latter is pushed back into the orbit. The ocular movements, however, are relatively sluggish, the eyes moving independently of each other.

¹ The painted turtle, *Chrysemys*, Detwiler (1943), etc.

The soft-shelled turtle, *Emyda*, Gillett (1923).

The common European fresh-water turtle, *Emys obicularis*, Vilter (1949).

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

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

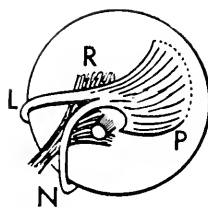


FIG. 453.—THE POSTERIOR SEGMENT OF THE GLOBE OF THE TURTLE.

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

THE CROCODYLIAN EYE

THE CROCODYLIA are the largest extant Reptiles, decadent survivors of the giant Reptiles which dominated the earth in Mesozoic times. Three genera are extant—the CROCODYLES, widely spread over tropical rivers in Africa, Asia, Central America and Australia, the ALLIGATORS



FIG. 454.—THE HEAD OF A YOUNG AMERICAN ALLIGATOR OF THE GENUS *CAIMAN* (R. M. Holmes).

of North and South America and China, and the fish-eating GAVIALS of the Ganges River. They are sluggish creatures, more motile on water than on land where most of them obtain their prey, fond of basking in the sun and prone to hide in mud in the hot season (Fig. 454). Their eyes, primarily nocturnal in their characteristics, are adapted for aerial vision for in their predominantly aquatic activities these reptiles float with the eyes and nostrils above the surface and the rest of the body awash. Their essential features are *the absence of scleral ossicles, the reduced accommodative musculature, the slit-pupil, the marked ciliary processes, the retinal tapetum, the rod-rich retina, and the rudimentary optic nerve.*



Gavial

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

The *ciliary body* shows more than 100 tongue-shaped ciliary processes² which contact the lens at its equator ; the ciliary musculature

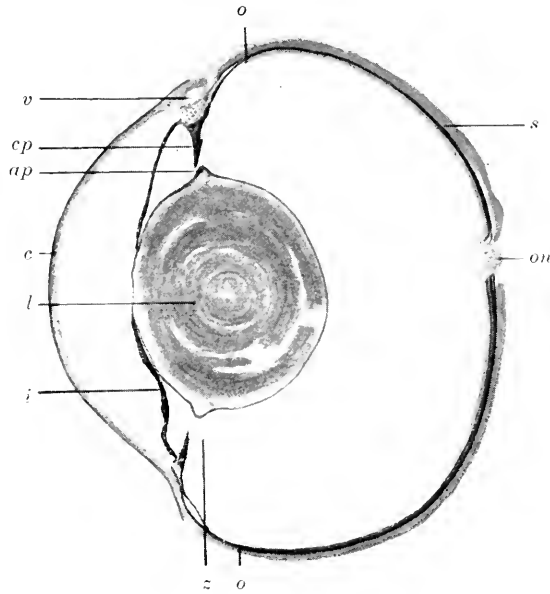


FIG. 455.—THE CROCODILIAN EYE.

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

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

¹ p. 356.

² 117 ciliary processes : Tiedemann, Oppel and Liposchitz, *Naturgeschichte der Amphibien*, Part I. Heidelberg (1817).

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

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

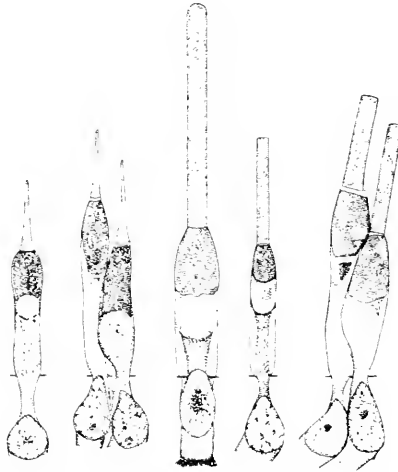


FIG. 456.—THE VISUAL CELLS OF CROCODYLIANS.

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

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

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



Crocodile

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

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

FIGS. 457 AND 458.—THE EYE OF THE ALLIGATOR.

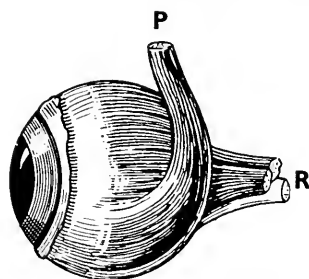


FIG. 457.—(After Bland-Sutton.)

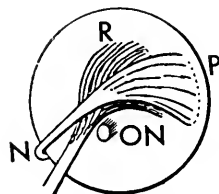


FIG. 458.—(After Franz.)

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

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

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

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

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

THE RHYNCHOCEPHALIAN EYE

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



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

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

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

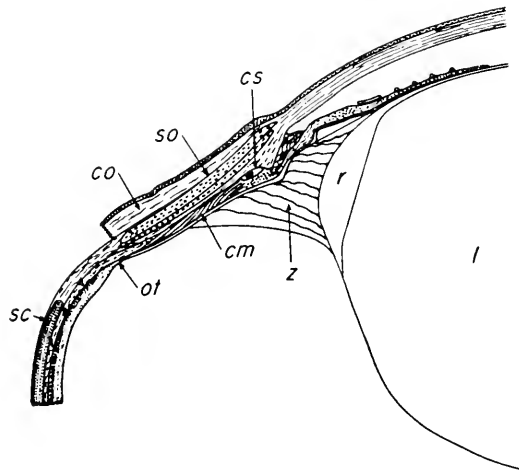


FIG. 460.—THE CILIARY REGION OF *SPHODON*.

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

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

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

PLATE VIII
THE EYES OF CROCODILIANS AND *SPHENODON*

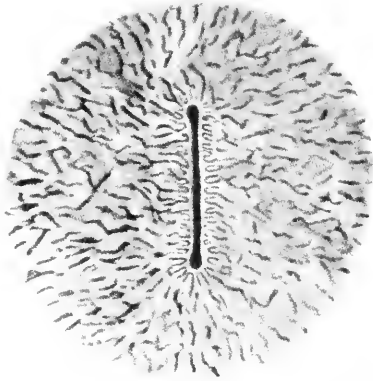


FIG. 1.—The iris of the broad-fronted crocodile,
Osteolemus tetraspis (Ida Mann).

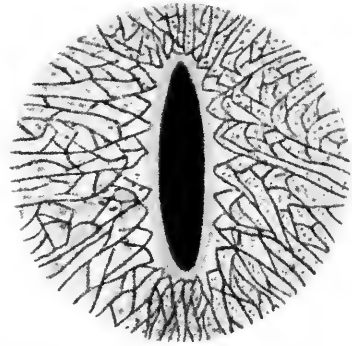


FIG. 2.—The iris of the spectacled cayman,
Caiman crocodilus (Ida Mann).

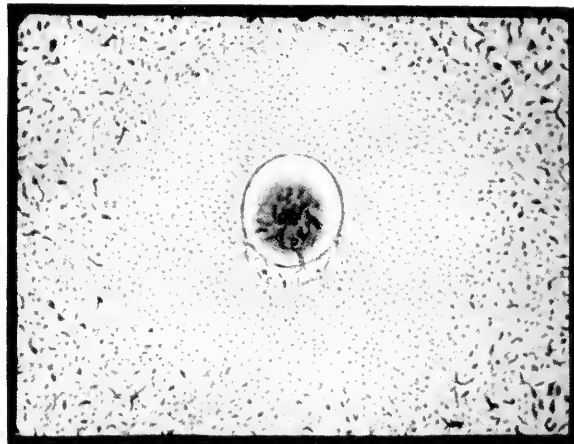


FIG. 3.—The fundus of *Alligator chinensis* (Lindsay Johnson).



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

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

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

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

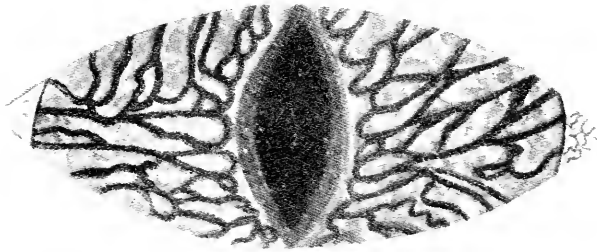


FIG. 461.—Showing the vascular arrangements (Ida Mann).

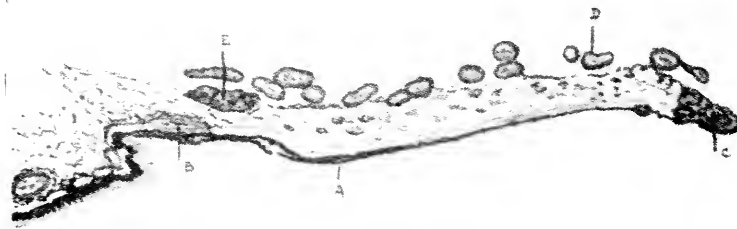


FIG. 462.—Showing the pigmentary epithelium, *A*, the sphincter muscle, *C*, and the peculiar vascular arrangements. Among these, *B* is an afferent vessel from the ciliary region, and *D* is one of the many arteries of the iris which float freely in the anterior chamber. *E* is a nerve trunk (Ida Mann).

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

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

¹ p. 651.

² Osawa (1898-99), Kallius (1898), Virchow (1901), Bage (1912), Mann (1932-33), Walls and Judd (1933), Walls (1934).

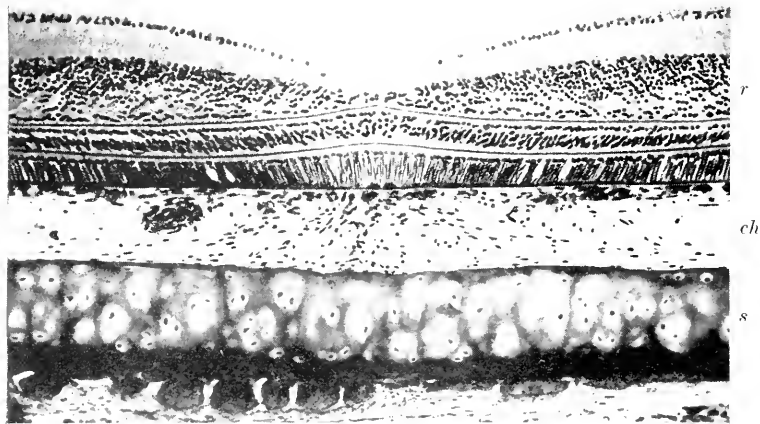


FIG. 463.—THE RETINA OF *SPHENODON* IN THE CENTRAL AREA. Showing the shallow fovea. *r*, retina; *ch*, choroid; *s*, scleral cartilage ($\times 90$) (Gordon Walls).

microscopically the fundus is reddish-brown with a stippling of golden spots whereon the arrangement of the white and relatively coarse nerve fibres is clearly delineated as they radiate uniformly outwards from the optic disc. Three visual elements are present, the majority of which were interpreted by the older writers as cones and are still held to be such by observers such as Vilter (1951) who found a relationship between the receptor and

ganglion cells of 1 : 1, as in the lizard. Walls (1934), on the other hand, claimed that the preponderant visual cells are rods with enlarged and sturdy outer segments, homologous with the cones of Chelonians and Crocodilians; single and double elements are present in approximately equal numbers, with colourless oil-droplets in the former and in one component of the latter (Walls and Judd, 1933). The third type of cell, a small and ill-formed cone without an oil-droplet, is sparse and absent from the fovea (Fig. 464). The central fovea is shallow but well-formed, and, if Walls's interpretation is accepted, shares with that of a gecko,¹ and some nocturnal primates,² the distinction of being the

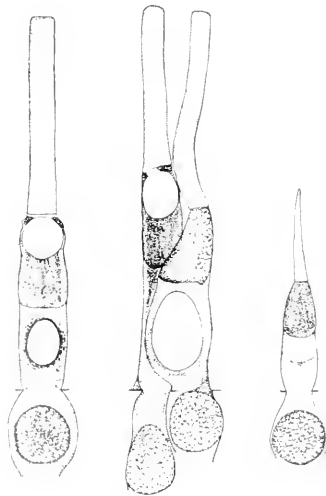


FIG. 464.—THE VISUAL CELLS OF *SPHENODON*.

A single "rod", a double "rod" and a cone ($\times 1,000$) (Gordon Walls).

¹ p. 365.

² p. 486.

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

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

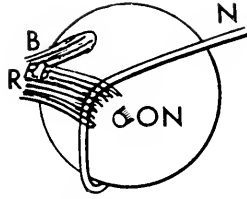


FIG. 465.—THE POSTERIOR SEGMENT OF THE GLOBE OF *SPHENODON*.

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

THE OPHIDIAN EYE

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

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

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

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

² p. 731.

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

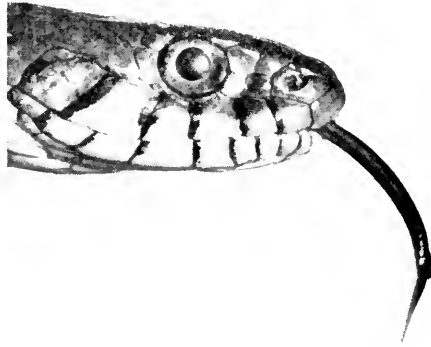


FIG. 466.—THE HEAD OF THE GRASS SNAKE *TROPIDONOTUS NATRIX* *NATRIX* (Katharine Tansley).

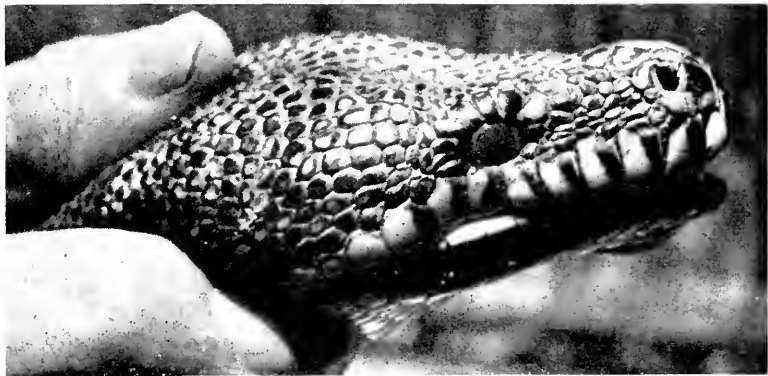


FIG. 467.—THE HEAD OF THE PYTHON, *SPILOTES VARIEGATUS*.
To show the spectacle (O'Day).

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

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

FIGS. 468 AND 469.—THE OPHIDIAN EYE.

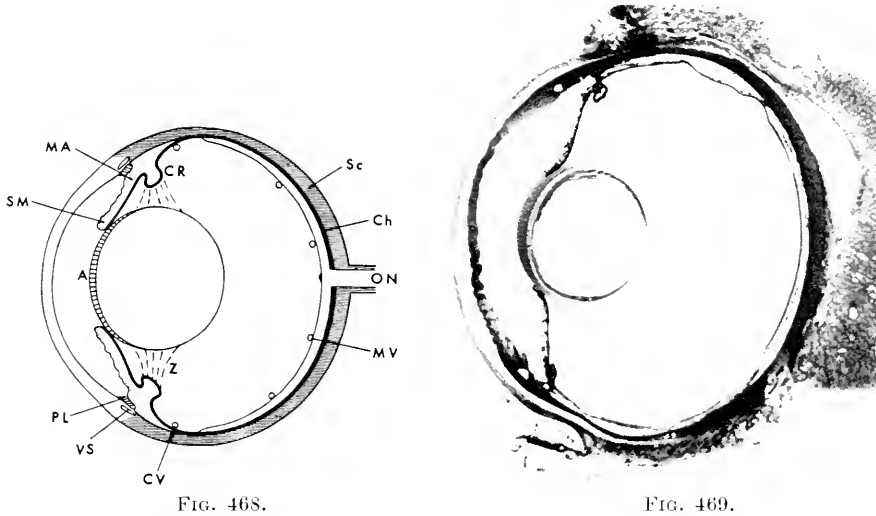


FIG. 468.

FIG. 469.

FIG. 468.—Diagram of an ophidian eye. *A*, anterior pad; *Ch*, choroid; *CR*, ciliary roll; *CV*, circular vein; *MA*, muscle of accommodation; *MV*, membrana vasculosa retinae; *ON*, optic nerve; *PL*, pectinate ligament; *Sc*, sclera; *SM*, sphincter muscle; *VS*, ciliary venous sinus; *Z*, zonule.

FIG. 469.—The eye of the tiger snake, *Notechis* (Norman Ashton).

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

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

¹ p. 266, Fig. 279.

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

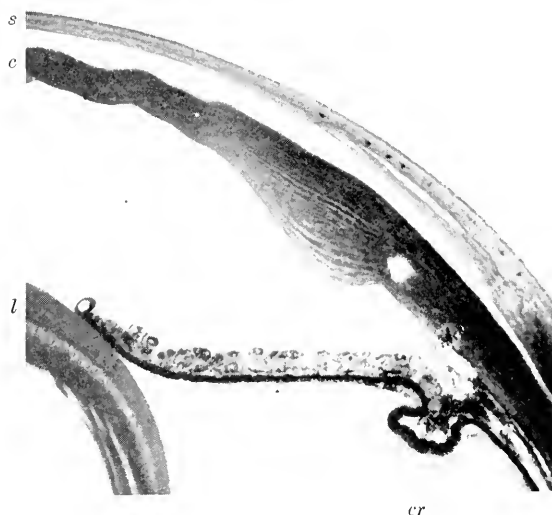


FIG. 470.—THE ANTERIOR SEGMENT OF THE EYE OF THE TIGER SNAKE.

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



Cobra

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

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

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

PLATE IX
THE IRIDES OF SNAKES
(Ida Mann)



FIG. 1.—Royal python, *Python regius*.

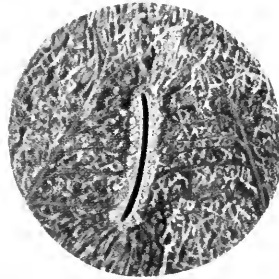


FIG. 2. Reticulated python, *Python reticulatus*.

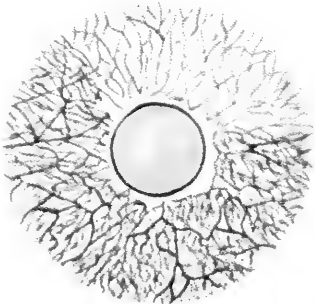


FIG. 3.—Four-line snake, *Elaphe quatuorlineata*.

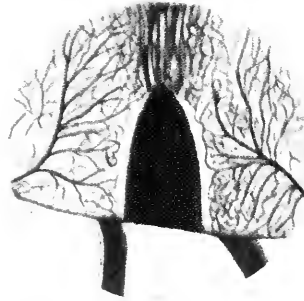


FIG. 4. Black-and-gold tree-snake, *Boiga dendrophila*. The edges of the brown and yellow scales below the eye are seen.

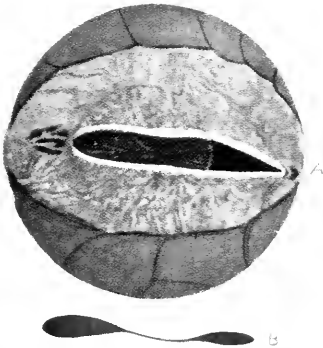


FIG. 5.—Emerald tree-snake, *Pseustes prasinus*. A, right eye; aphakic area on right. The outline of the lens can be seen. The green scales surrounding the eye are shown. B, the shape of the pupil when contracted.

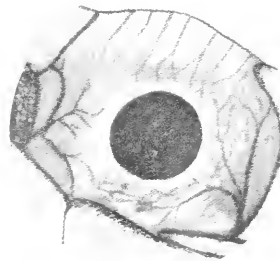


FIG. 6.—Chicken-snake, *Elaphe quadrivittata*. The edges of the scales bordering the eye are also shown.

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

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

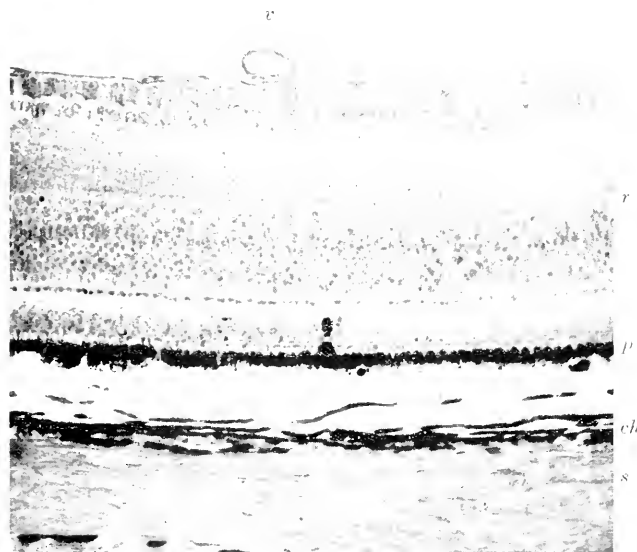


FIG. 471.—THE POSTERIOR SEGMENT OF THE GLOBE OF THE COPPERHEAD SNAKE.

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

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

The musculature of the iris is mesodermal and derived from the ciliary region. Circular fibres predominate, being concentrated into two accumulations, one near the pupil to form a relatively compact mass acting as a sphincter, the other at the root acting as a muscle of



Copperhead
(crotalid snake)

accommodation ; the dilatator fibres lie beneath these and run radially towards and sometimes into the ciliary body. The pupils are usually very active since they assume the light-protective function in the absence of movable lids ; in some types, however, the contraction is slight (*Python*) or even absent (the European grass-snake, *Tropidonotus natrix* ; the Madagascar sharp-nosed snake, *Heterodon madagascariensis*). Probably because of the impermeability of the corneal spectacle, the instillation of miotic or mydriatic drugs is without effect (Johnson, 1927). In nocturnal and burrowing snakes (with few excep-

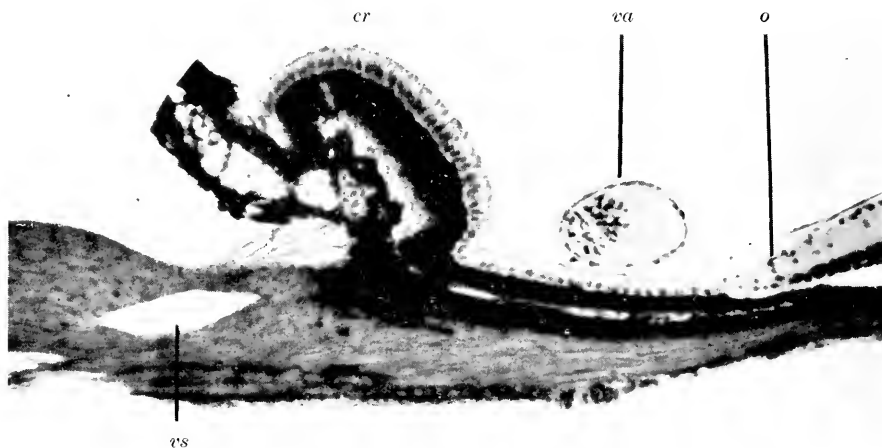


FIG. 472.—THE CILIARY REGION OF THE GRASS SNAKE, *TROPIDONOTUS NATRIX NATRIX*.

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

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

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

The lens is subspherical (1.1–1.25), is firmer in consistency than in *Ophidia*. Reptiles. is provided with sutures, and instead of an equatorial

¹ p. 304.

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

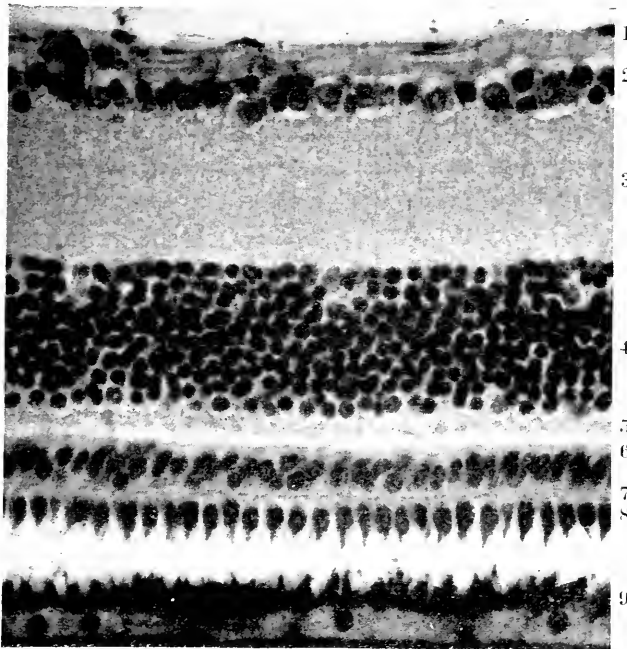


FIG. 473.—THE RETINA OF THE GRASS SNAKE, *TROPIDONOTUS NATRIX*.

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

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

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

¹ p. 648.

sionally, particularly in the Indian python, *Python molurus*, choroidal vessels somewhat resembling those seen in the human eye are evident in the periphery of the fundus. The optic disc is always round and

white, although it varies much in size; that of the water-snake, *Tropidonotus fasciatus*, is enormous, exceeding in size that of any Vertebrate with a circular disc, even that of the whales in which the eye may reach a diameter of $5\frac{1}{2}$ inches. Usually on the surface of the disc there is some melanin pigment, sometimes in small quantity (Boidæ), sometimes associated with a cushion of mesoderm, resembling the appearance seen in Crocodilians (Beauregard, 1876; Kopsch, 1892; Leplat, 1922; Jokl, 1923). This, representing the remains of mesoderm entering with the hyaloid vessels, is functionless and is not homologous with the neuroglial conus of lizards although in certain species it may project into the vitreous to form a very similar structure (pigmented in the British adder, *Vipera berus*; colourless in the king-snake, *Lampropeltis*). The remains of the hyaloid vasculature, however, form a well-defined system of vessels, three and sometimes four of which emerge through the disc from the optic nerve. In some species these are small and are apparent only a short distance from the disc (Boidæ); more usually arteries of considerable size run nasally and temporally, drain into two

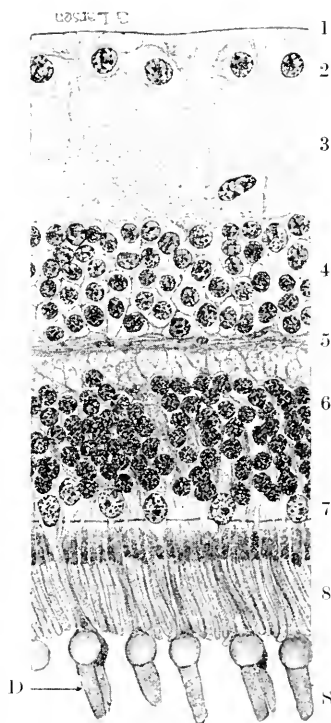


FIG. 474.—THE RETINA OF *LEPTODEIRA ANNULATA*.

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

venous arcs which encircle the globe in the region of the orbitulus, and combine to form a hyaloid vein which runs backwards in the fundus mid-ventrally to leave the eye at the optic disc. Over the surface of the retina lying in the vitreous there is a MEMBRANA VASCULOSA of very fine capillaries (Fig. 471) (Hyrtl, 1861; Virchow, 1901; Szent-Györgyi, 1914); only in the colubrid snake, *Tarbophis*, are these known to penetrate the vitreous itself.¹

Cf. the direct vascularization of the retina of the eel, p. 300.

PLATE X
THE FUNDI OF SNAKES
(Lindsay Johnson)

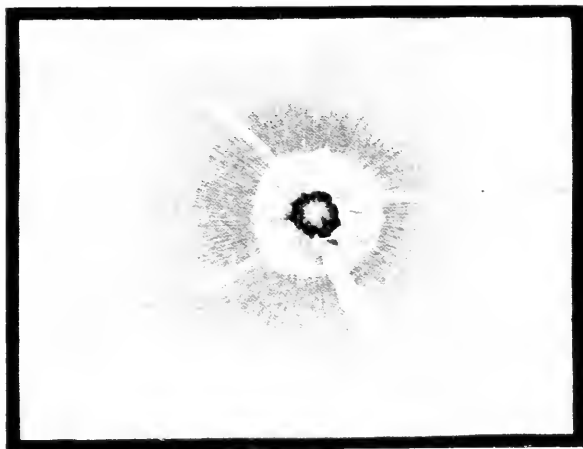


FIG. 1.—The sharp-nosed snake, *Hebirodon montanus*.

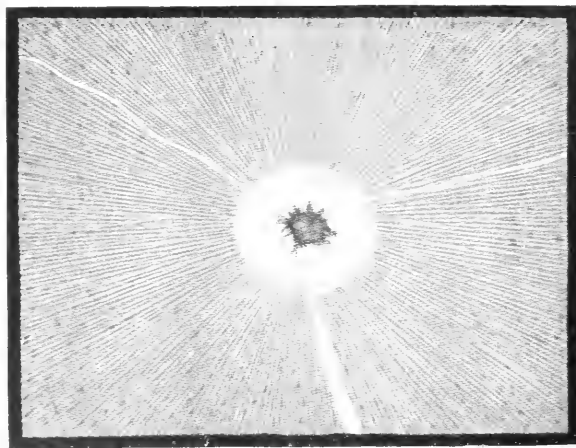


FIG. 2. The Indian cobra, *Naja tripudians*.

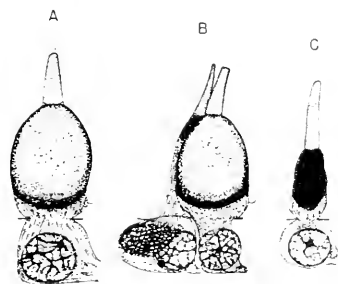


FIG. 475.—The 3 cone-types (A, B, C) constituting the fundamental pattern in diurnal forms (drawn from the European grass snake, *Tropidonotus natrix*).

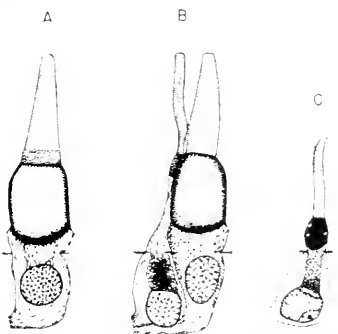


FIG. 477.—Visual cell types of scotopic colubrids.

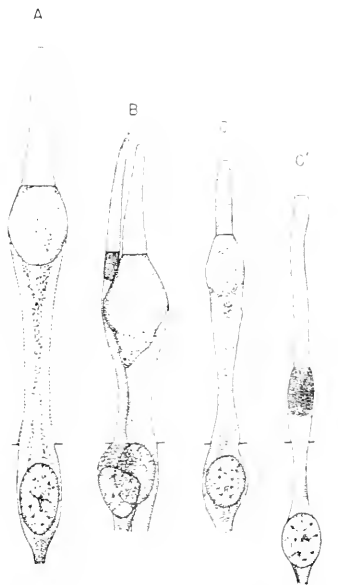


FIG. 479.—Visual cell types of the African puff-adder, *Bitis arietans* (strongly nocturnal in habit). The Type C' (rod) is the most abundant element.

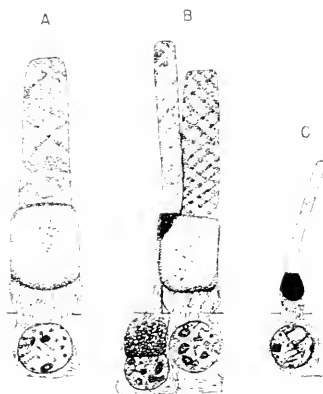


FIG. 476.—The 3 rod-types in the spotted night snake, *Hypsiglena*.



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

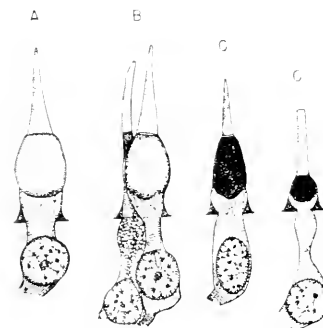


FIG. 480.—Visual cell types of the Cape viper, *Causus rhomboides* (crepuscular in habit). There are two variations of Type C, Type C' (rod) being most abundant.



Head of
Dasypeltis



Head of the
horned viper



Head of the
puff adder

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

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

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

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

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

388.

³ p. 314.

⁴ p. 266.

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

When the snake sheds its skin the milky layer which forms under the stratum corneum throughout the body is very obvious through the transparent spectacle ; and with the skin the spectacle is also shed, leaving a free ragged border on its inner surface where it was attached at the sclero-corneal junction. So tough is this thin layer of skin (0.1 mm. thick) that it still retains its hemispherical form after it has been discarded ; meantime, the snake lies sluggish and irritable and seeks no food.

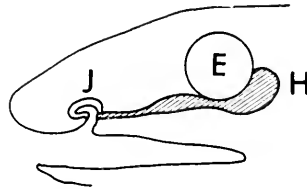


FIG. 481.—THE HARDERIAN DUCT OF A SNAKE.

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

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

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

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

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¹ See p. 695.

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

CHAPTER XIV

THE EYES OF BIRDS

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

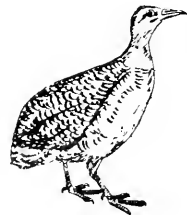
BIRDS, descendants of primitive Reptiles probably through the Dinosaurs,¹ are essentially adapted for the air for which purpose their forelegs are modified as wings. The extant species are divided into two main classes:

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

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



Emu



Tinamou

¹ p. 234.

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



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



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



FIG. 485.—Persian eagle, *Geranoaëtus* (photography Michael Soley).



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

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

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

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

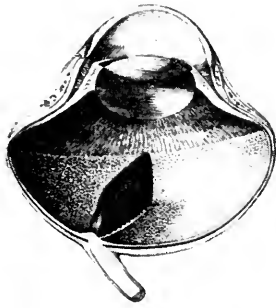


FIG. 487.—The falcon.



FIG. 488.—The owl.

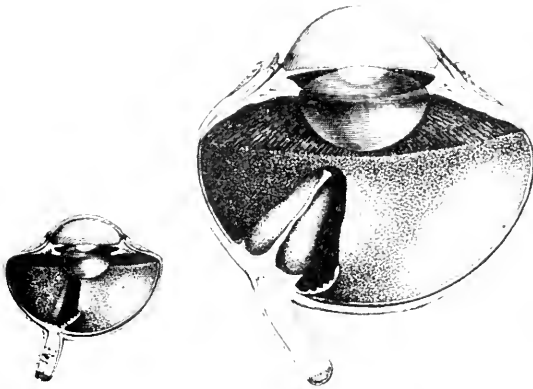


FIG. 489.—The parrot.

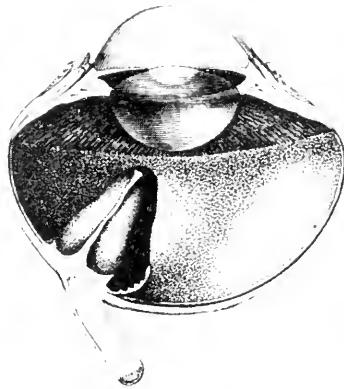


FIG. 490.—The ostrich.

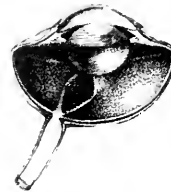


FIG. 491.—The swan.

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

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

THE EYE IN EVOLUTION

FIGS. 492 AND 493.—THE AVIAN EYE.

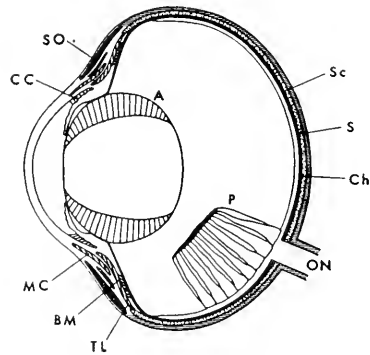


FIG. 492.—Diagram of the eye of a bird.

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

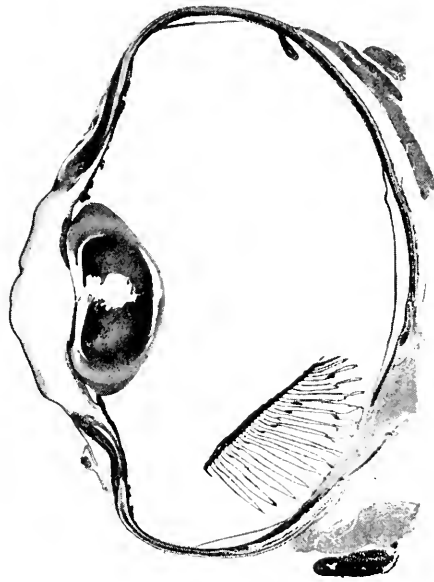


FIG. 493.—The eye of the domestic chicken (Norman Ashton).

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

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

The large size of the eye¹ and its flattened, globular or tubular shape with a nasal eccentricity of the cornea and lens to assist binocular vision.

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

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

A lens with a well-defined annular pad.

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

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

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

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



Grouse

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

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

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



Thrush

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



Raven

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

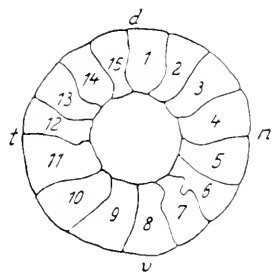


FIG. 495.—THE RING OF SCLERAL OSSICLES OF THE RIGHT EYE OF THE GOSHAWK, *ASTUR PALUMBARIUS*.
d, dorsal; v, ventral; n, nasal;
t, temporal (after Franz).



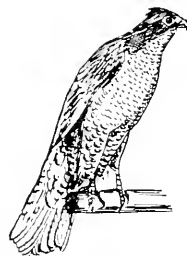
FIG. 496.—THE CARTILAGINOUS CUP IN THE POSTERIOR PART OF THE GLOBE OF THE HAWK.

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

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



Magpie



Goshawk
Astur



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

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

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



The cormorant
Phalacrocorax

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

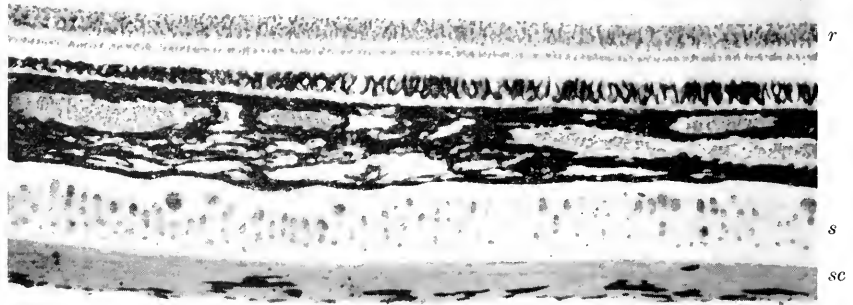


FIG. 498.—THE POSTERIOR SEGMENT OF THE GLOBE OF THE CHICKEN.
r, retina ; ch, choroid ; s, scleral cartilage ; sc, sclera ($\times 80$) (Norman Ashton).

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



The heron
Ardea

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

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

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

The vascular layer of the choroid is continued forwards into the *ciliary region* without the intervention of an orbiculus, the whole zone being occupied by the numerous elongated ciliary processes: ventrally, in the region of the foetal cleft, it is claimed that a particularly marked CILIARY CLEFT between the processes allows communication between the anterior and posterior chambers (Nüssbaum, 1901; Hess, 1912; Ischreyt, 1914). The ciliary processes and their associated uveal tissue angle sharply inwards to approach the lens, while the ciliary muscles cling closely to the sclera, thus separating the two components of the ciliary body and leaving a deep cleft-like space between the two layers traversed by the strands of the pectinate ligament (Fig. 499). The ciliary musculature, which is made up of striated fibres, resembles that of the lizard in its topography¹ (Fig. 500): both it and the muscles of the iris are supplied by a complicated plexus of motor and sensory nerves (Boeke, 1933). The meridional muscular bundle appears to be divided into two; anteriorly the MUSCLE OF CRAMPTON, a stout muscular band, arises from the inner surface of the cornea at its margin and is inserted into the sclera as it bulges axially in the ciliary region; more posteriorly BRÜCKE'S MUSCLE, arising from the inner aspect of the sheet of sclera which forms the anchorage of the pectinate ligament, is inserted into the posterior portion of the ciliary body, an insertion which is prolonged to the sclera by the TENACULAR LIGAMENT, thus relieving the choroid of mechanical strain. Accommodation, as in lizards, is mainly effected by the contraction of the meridional musculature forcing the ciliary body against the lens so as to deform it, tautening the fibres of the pectinate ligament meanwhile (Wychgram, 1913-14). Simultaneously the stout Crampton's muscle running from the cornea to the sclera like a bow-string, deforms the cornea and shortens its radius of curvature, an action much more pronounced in Birds than in lizards.



The ostrich
Struthio

¹ p. 357.

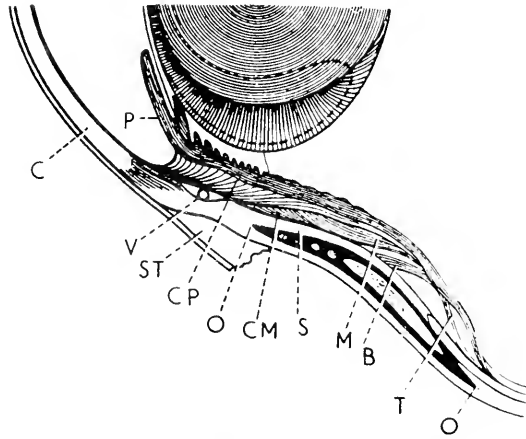


FIG. 499.—THE CILIARY REGION OF THE GOSHAWK, *ASTUR PALUMBARIUS*.

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

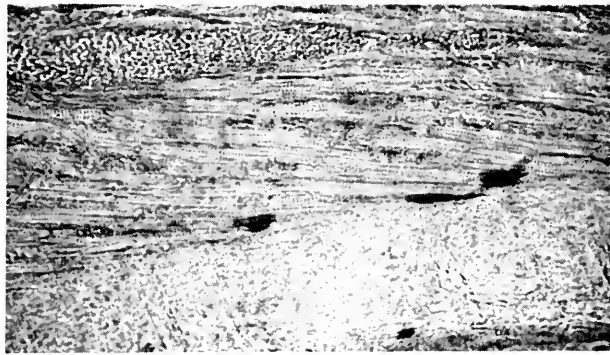


FIG. 500.—THE STRIATED FIBRES OF CRAMPTON'S MUSCLE IN THE CHICKEN ($\times 240$) (Norman Ashton).



The cassowary
Casuarus

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

PLATE XI
THE IRIDES OF BIRDS
(Ida Mann)

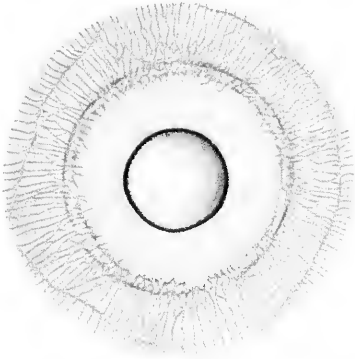


FIG. 1.—Jackdaw (albino), *Colaptes monedula*.

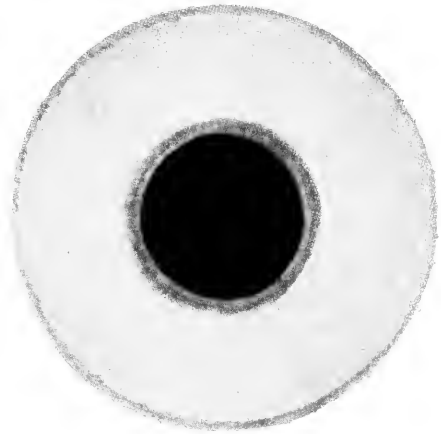


FIG. 2.—Pigeon, *Columba*.

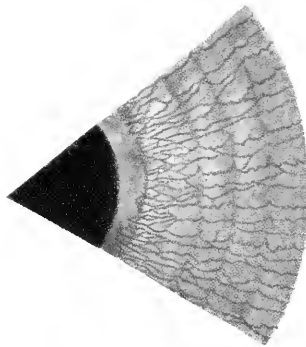


FIG. 3.—Duck, *Dendrocygna*.

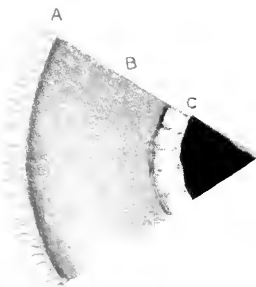


FIG. 4.—Rock-hopper penguin, *Eudyptes chrysater*.

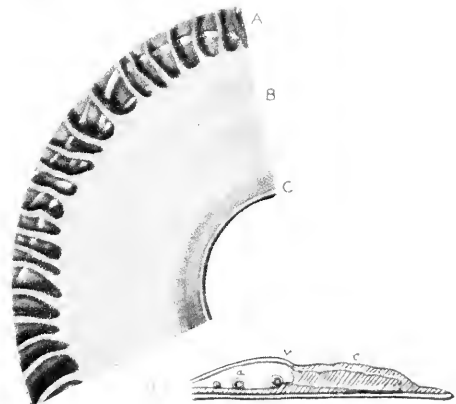


FIG. 5.—Scops owl, *Otus bakkamana*.

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

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

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

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



The swift
Micropus



The gannet
Sula



The shearwater
Puffinus



The flamingo
Phoenicopterus



The penguin
Eudyptes

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

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

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

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

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



The house-sparrow
Passer domesticus

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

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

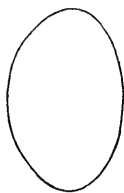


FIG. 501.—The pigeon.

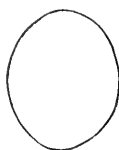


FIG. 502.—The owl.



FIG. 503.—The bullfinch.

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

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

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

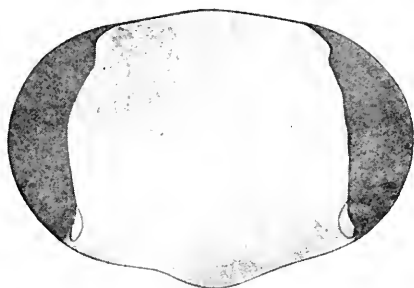


FIG. 504.—The lens of a diurnal predator (a hawk). Showing a very large annular pad.

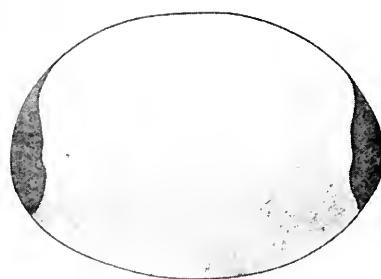


FIG. 505.—The lens of a nocturnal bird (an owl). Showing a small annular pad.

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

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

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

The PECTEN,¹ originally described by

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



The goat-sucker
Caprimulgus



The ostrich
Rhea



The bald eagle
Haliaeetus



The pelican
Pelecanus

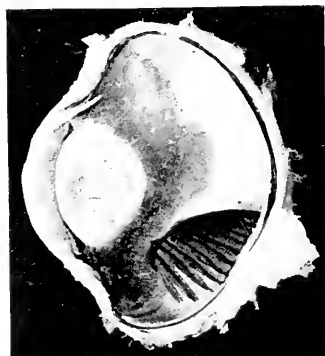


FIG. 506.—VERTICAL SECTION OF THE RIGHT EYE OF A GOOSE.

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

PLATE XII
THE FUNDI OF BIRDS



FIG. 1.—The kiwi, *Apteryx mantelli*.



FIG. 2.—The tawny owl, *Strix aluco*.



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

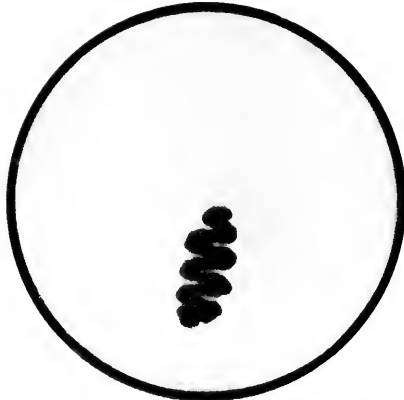


FIG. 4. The European nightjar, *Caprimulgus europaeus*.



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



FIG. 6. The albatross, *Diomedea*.

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

$\frac{1}{2}$

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

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

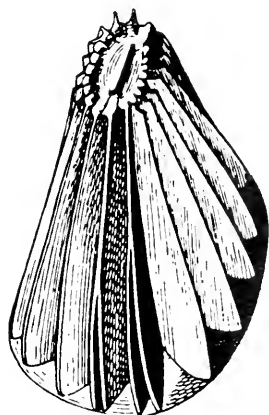


FIG. 507.—Diagram of the pecten of the ostrich, *Struthio* (x 5).

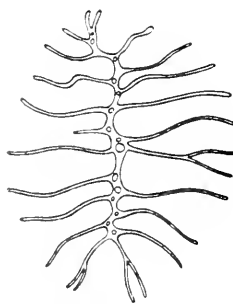


FIG. 508.—Section parallel to the base showing the central web and the lateral vanes (after Franz).

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

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

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

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



The kiwi
Apteryx

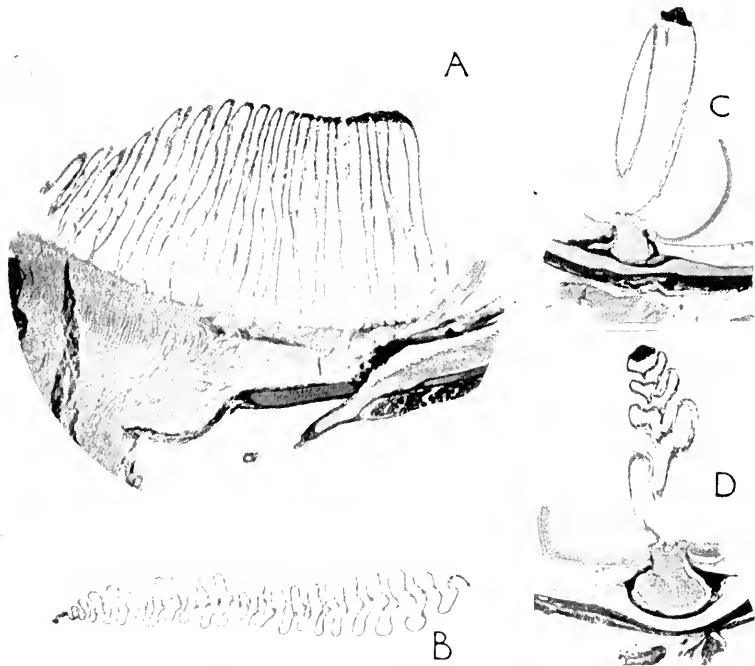


FIG. 509.—THE PLEATED TYPE OF PECTEN.

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

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

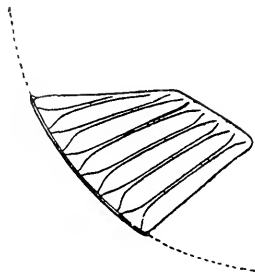


FIG. 510.—THE SIMPLE PLEATED PECTEN OF THE BARN OWL, *STRIX* (Casey Wood).

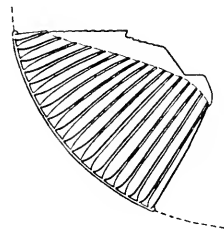


FIG. 511.—THE ELABORATE PLEATED PECTEN OF THE RED-HEADED WOODPECKER, *MELANERPES ERYTHROCEPHALUS*.

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

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

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

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

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

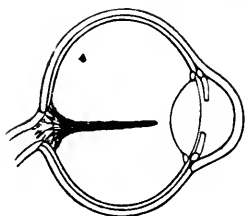


FIG. 512.—The kiwi,
Apteryx.

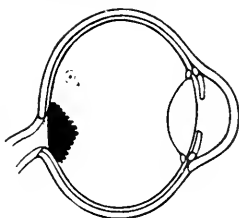


FIG. 513.—The common
kestrel, *Falco tinnunculus*.

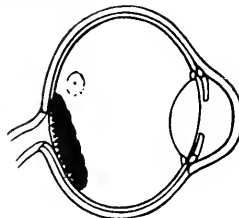


FIG. 514.—The secretary
bird, *Serpentarius*.

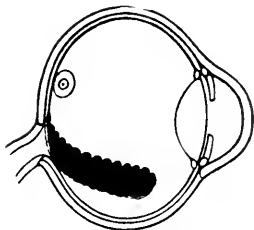


FIG. 515.—The herring-
gull, *Larus argentatus*.

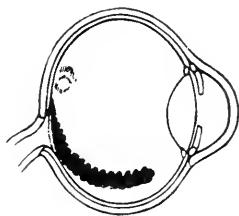


FIG. 516.—The wood-
pigeon, *Columba
palumbus*.

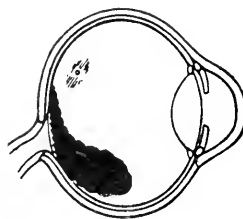


FIG. 517.—The American
ostrich, *Rhea*.

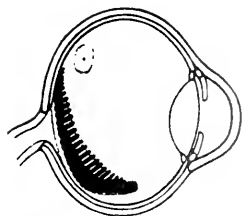


FIG. 518.—The laughing
kingfisher, *Dacelo gigas*.

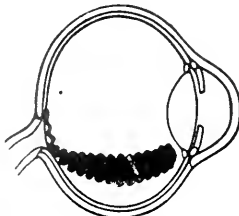


FIG. 519.—The chimney
swallow, *Hirundo rustica*.

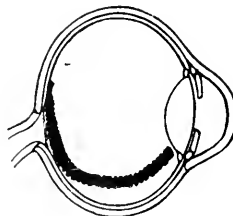


FIG. 520.—The blue jay,
Cyanocitta.



The night heron
Nycticorax



The secretary bird
Serpentarius



The blue jay
Cyanocitta

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

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



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



The swallow
Hirundo

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

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



The woodpecker
Dendrocopus
major

¹ Mihalkovics (1873), Denissenko (1881), Bernd (1905), Franz (1908-9), Blochmann v. Husen (1911), Ischreyt (1914), Kajikawa (1923), Mann (1924), Menner (1935), Ika (1938).

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

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

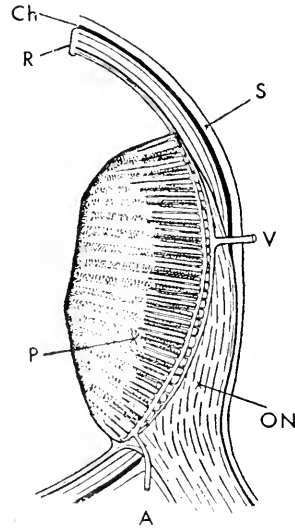


FIG. 522. —THE STRUCTURE OF THE PECTEN.

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

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

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

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

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

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

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

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

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

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

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

¹ p. 63.

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

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

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

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

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



Hawk,
Buteo



Kingfisher,
Alcedo



Winchat,
Saxicola



Californian quail,
Lophortyx

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

² Compare the lizard, *Anolis*, p. 365.

³ p. 641.

⁴ Lat. *infula*, a band (Casey Wood, 1917).



Owl-parrot,
Stringops

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

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



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

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

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

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



Albatross,
Diomedea

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

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

Histologically the retina of birds is the most beautiful and elaborate in its architecture in the animal kingdom¹ ; layers and sub-layers are clearly defined with each cell accurately in place (Fig. 523). As with other Sauropsida the pigmentary epithelial cells send slender processes containing fuscine granules extending inwards to the inner segments of the visual cells ; their movements with variations of light and shade are rapid and extensive, possibly making up for the relative inertia of the pupil to light. In the visual retina the ganglion cells lie in 2 or 3 rows. The inner plexiform layer is unusually thick and stratified at the levels at which the arborizations of the amacrine cells deploy. The inner nuclear layer is expanded to have three strata—innermost the (integrative) amacrine cells which may even outnumber the bipolars, outermost the (conductive) bipolar elements, and in the middle a single compact row of Müller's fibres. This layer as a whole is thus very thick, and mainly because of the unusual development of this and the inner plexiform layer, the retina of Birds is some one-and-a-half times to twice as thick as that of the majority of Vertebrates, being approached in this respect only by a few Teleosteans.

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



Tern,
Sterna

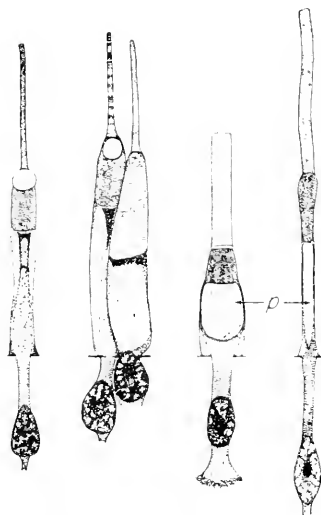


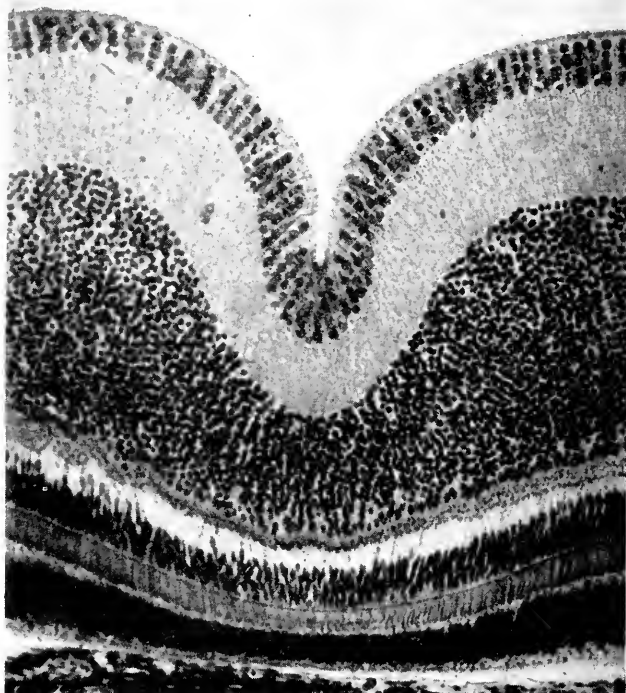
FIG. 524.—THE VISUAL CELLS OF BIRDS.

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

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

Kite, *Milvus*

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

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

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

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

Stormy petrel,
Procellaria

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

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

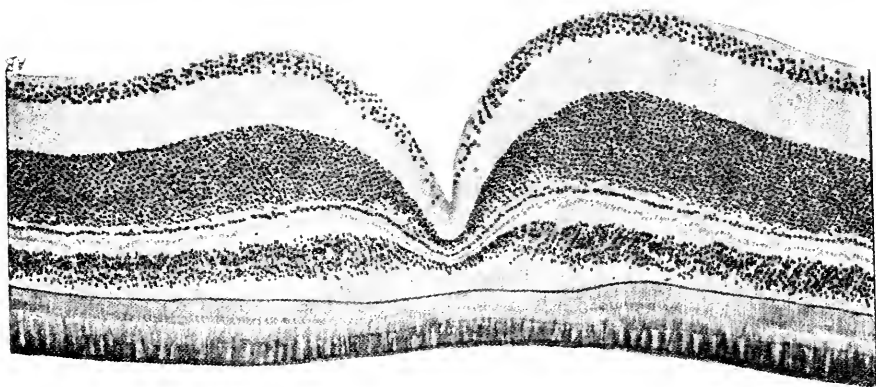


FIG. 526.—THE CENTRAL FOVEA OF THE SWALLOW, *HIRUNDO*.
(Rochon-Duvigneaud).

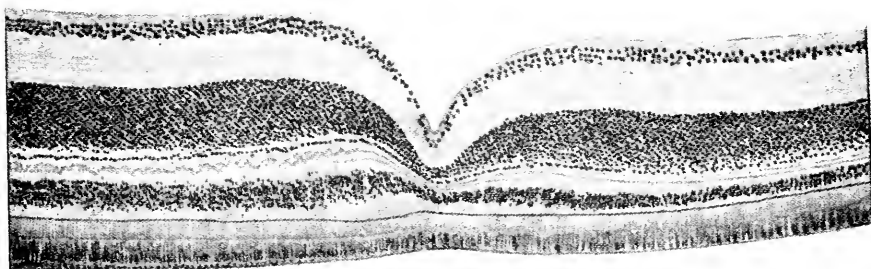


FIG. 527.—THE LATERAL FOVEA OF THE SWALLOW, *HIRUNDO*.
(Rochon-Duvigneaud).



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

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

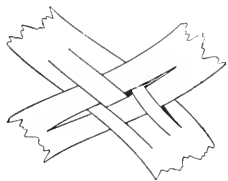


FIG. 529.—THE DECUS-SATION AT THE CHIASMA OF A BIRD.

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

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

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



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

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

¹ p. 658.

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

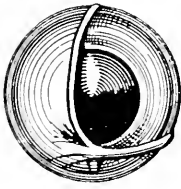


FIG. 531.—The anterior aspect of the eye of the turkey.

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

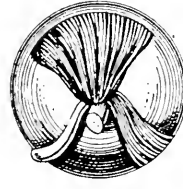


FIG. 532.—The posterior aspect of the eye of the turkey.

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

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

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

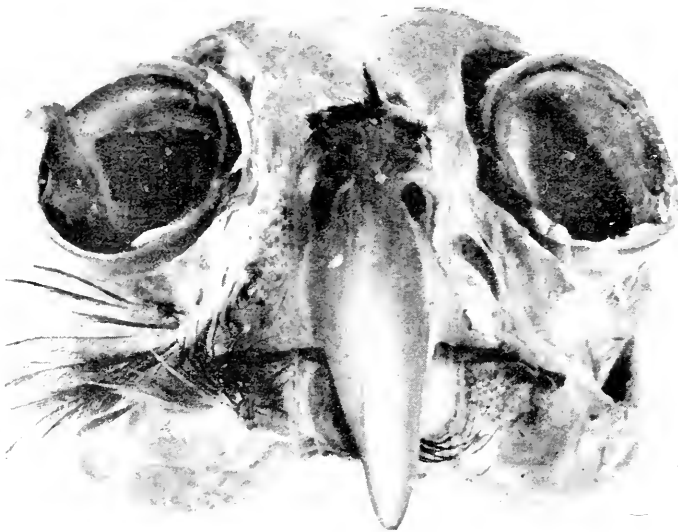


FIG. 533.—THE ORBITS OF THE SPARROWHAWK, *ACCIPITER*.

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

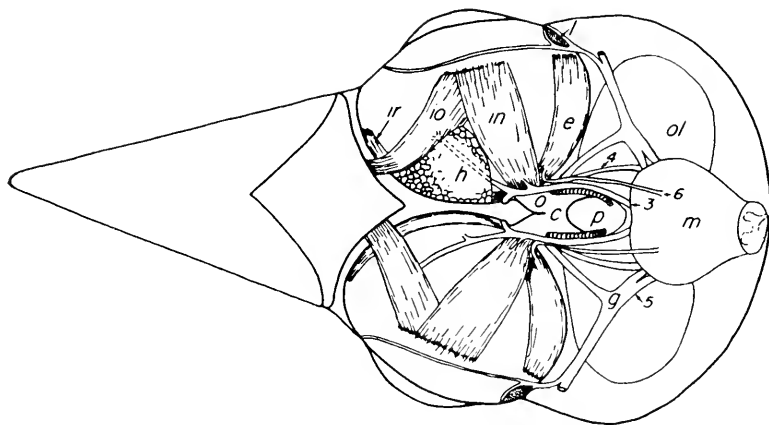


FIG. 534.—THE ORBITS AND BRAIN OF THE ENGLISH SPARROW, *PASSER DOMESTICUS*.

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

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

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

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

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

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

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

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

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¹ p. 643.

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

³ p. 696.

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Sept 17/1920

Yours most sincerely
Geo Lindsay Johnson

FIG. 535.—GEORGE LINDSAY JOHNSON (1853-1943).

CHAPTER XV

THE EYES OF MAMMALS

The portrait of GEORGE LINDSAY JOHNSON (1853-1943) (Fig. 535) seems to be a suitable introduction to this chapter on the mammalian eye. He was one of those extraordinary people whose life was full of interest and odd happenings. Born in England, in Manchester, he received much of his early education in Germany and for that purpose was in Strasbourg when it was taken by the Germans in 1870. Thereafter he completed his medical studies and ophthalmic training in London, leaving in 1911 for South Africa where he died at the age of 90. In London he spent most of his spare time in the Zoological Gardens where he studied intensively the comparative anatomy of the eye, making contributions to the Royal Society on the eyes of Reptiles, Amphibians and Mammals. This interest he maintained to the end. So enthusiastic, indeed, was he that at an advanced age, determined to observe the fundus of the whale in life, he joined a whaling expedition, had a special crane built on the deck of the ship and had himself lowered over the back of the animal so that he could sketch its fundus. His *Pocket Atlas of the Fundus Oculi* is well known; and his extraordinary versatility is exemplified in the many optical instruments which he devised as well as his pioneer work in colour photography, a subject in which he maintained an interest to the end of his life.

MAMMALIA, the highest class of the Vertebrates, have evolved from primitive Reptiles on diverging lines from the Birds¹; both classes show high adaptations, and if the Birds possess the air, Mammals possess the earth although a few have taken to the air and more to the trees, while others have become amphibious or aquatic. The Mammals, however, have two distinctive peculiarities—the elaboration of the brain and the intimate organic connection between mother and offspring. They possess in common several characteristic features—a covering of hair, a diaphragm and a four-chambered heart, three auditory ossicles and a three-chambered ear, a single jaw-bone, and—a circumstance peculiar to Mammals—the young are nourished by milk secreted from the female mammary gland. The eyes are not so fully developed as those of Birds, but their comparative anatomical simplicity is more than compensated functionally by the efficiency of the central nervous organization of vision.

From the ocular point of view—and from practically every other point of view—the extant members of the class are divided into three subclasses, which, it should be remembered, are not linearly derived the one from the other:

(1) The PROTOTHERIA or MONOTREMES which are oviparous, the young being hatched from eggs outside the body.

(2) The METATHERIA or MARSUPIALS, in which the young are born in an immature state and are (generally but not invariably) nourished and protected for some time in an external pouch (or marsupium).

(3) The EUTHERIA or PLACENTALS, in which the young are nourished within the uterus through the placenta until development is far advanced. It is among the Placentals that cerebral advancement begins to be marked.

¹ p. 234.



FIG. 536.—THE PLATYPUS, *ORNITHORHYNCHUS* (from Burton's *Story of Animal Life*, Elsevier Pub. Co.).



FIG. 537.—THE ECHIDNA, *TACHYGLOSSUS* (from Burton's *Story of Animal Life*, Elsevier Pub. Co.).

The eyes of these three types differ considerably, those of the first two, particularly the Monotremes, exhibiting many features characteristic of their reptilian ancestors adapted for nocturnality.

THE MONOTREME EYE

THE MONOTREMES are the most primitive of Mammals and include two types (Figs. 536-7) : the duck-mole or duck-billed platypus (*Ornithorhynchus*), found in the rivers and lakes of Australia and Tasmania, a shy creature with an enormous flat bill, which spends most of its time grubbing for small animals in the muddy bottoms ; and the spiny ant-eaters (the echidna, *Tachyglossus*, found in Australia, New Zealand and New Guinea, and its near relative, *Zaglossus*, found only in New Guinea), nocturnal ant-eating creatures burrowing in rocky regions. Neither relies primarily on vision ; the platypus relies largely on hearing, the eyes being closed when submerged, but the vision appears to be acute during

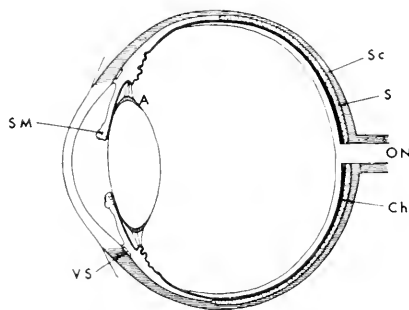


FIG. 538.—DIAGRAM OF A MONOTREME EYE.

A, small annular pad ; Ch, choroid ; ON, optic nerve ; S, scleral cartilage ; Sc, sclera ; SM, sphincter muscle ; VS, ciliary venous sinus.

the twilight hours. Vision can be only of secondary importance to the nocturnal ant-eater with its keratinized cornea.

The monotreme eye has many affinities with the eyes of Reptiles which it resembles much more than the typical eye of Mammals ; the eye, indeed, is that of a reptile in a mammal. There are only two outstanding differences between it and the reptilian eye. The first concerns the intra- and extra-ocular musculature, the former being confined to a sphincter of smooth fibres, the latter including a superior oblique muscle arising from the apex of the orbit. In the second place, the (otherwise typically reptilian) retina is completely avascular without any cone-like structure nor any participation of a hyaloid system in its nutriment. There has, however, been comparatively little work devoted to the subject—Marcus Gunn (1884) (the specimen sent from Australia to London preserved in Scotch whisky), O'Day (1938-52) and Newell (1953) on *Ornithorhynchus*, and Owen (1868) (macro-

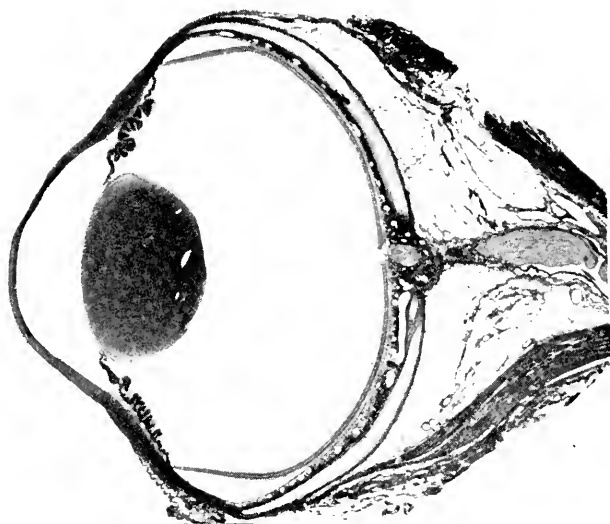


FIG. 539.—THE EYE OF THE PLATYPUS, *ORNITHORHYNCHUS* ($\times 11$) (O'Day).



540.—THE EYE OF THE ECHIDNA, *TACHYGLOSSUS* ($\times 7$) (O'Day).

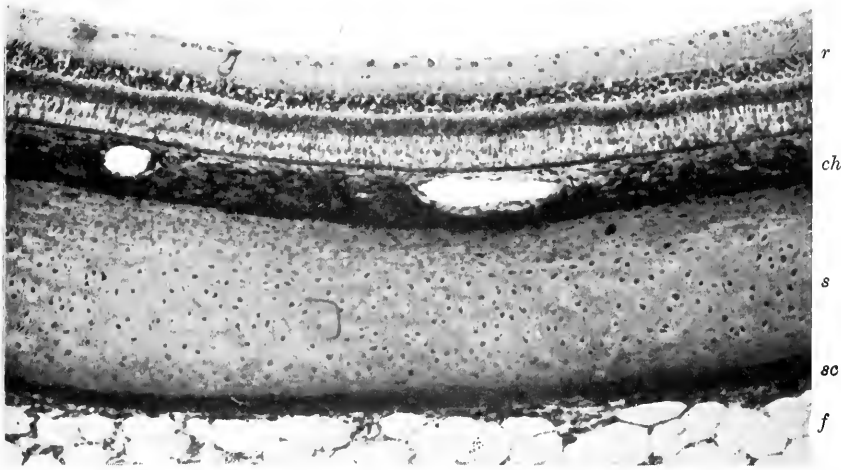


FIG. 541.—THE POSTERIOR SEGMENT OF THE GLOBE OF THE PLATYPUS.
ch, choroid ; *f*, orbital fat ; *r*, retina ; *s*, scleral cartilage ; *sc*, fibrous sclera (× 126) (O'Day).

scopic examination), Kolmer (1925-36), Franz (1934), Gresser and Noback (1935) and O'Day (1938-52) on the echidna (Figs. 538 to 540).

THE GLOBE OF THE EYE is roughly spherical, the sclera, as in most Reptiles, having a well-formed cartilaginous cup extending forwards to a little behind (*Tachyglossus*) or to the level of the ora (*Zaglossus*) or to the level of the ciliary processes (*Ornithorhynchus*) ; it is perforated to allow the transmission of the optic nerve, and the intra-ocular vessels and nerves (Fig. 541). This is the only instance of a scleral cartilage among the Mammals.¹ The corneal epithelium of the echidna is heavily keratinized like that of other ant-eaters (the armadillo, *Xnarthia*, and the aard-vark, *Orycteropus*), possibly as a protection against the formic acid with which ants defend themselves. As in aquatic Vertebrates generally, the corneal epithelium of the platypus is thick and Bowman's membrane is absent. The anterior ends of the ciliary processes are connected by a shelf-like structure running circumferentially around the globe (the *Sims* of Virchow, 1886 ; the

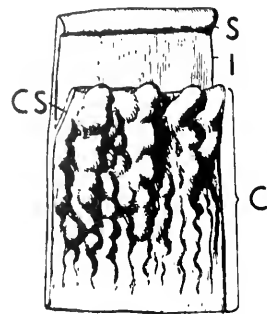


FIG. 542.—THE CILIARY PROCESSES OF ECHIDNA

C, ciliary body ; CS, ciliary shelf ; I, iris ; S, sphincter muscle (after Franz, 1911).

¹ With the exception of the cartilaginous nodules in *Notoryctes*, p. 438.

FIGS. 543 AND 544.—THE CILIARY BODY OF MONOTREMES.



FIG. 543.—The ciliary body of the platypus.

Note the large ciliary venous sinus in the connective tissue filling the angle of the anterior chamber. The small annular pad in the lens is seen to the right (O'Day).



FIG. 544.—The ciliary body of the echidna.
The ciliary venous sinus is much smaller (O'Day).

ciliary web of Walls, 1942)—a mammalian characteristic (Fig. 542). As in Sauropsida generally, the connective tissue of the ciliary region runs forwards to be inserted into Descemet's membrane and embedded in this lies the ciliary venous sinus, a structure more pronounced in Placentals¹ (Fig. 543). The brown *iris* is tenuous, consisting merely of

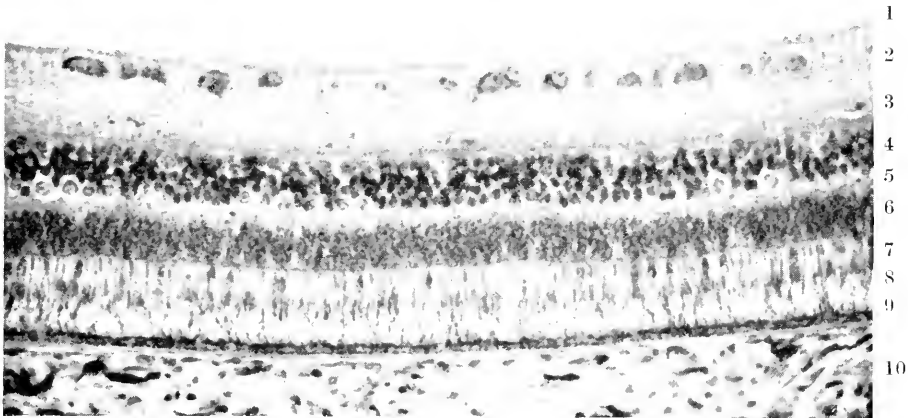


FIG. 545.—THE RETINA OF THE PLATYPUS.

1, optic nerve fibre layer ; 2, ganglion cells ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells ; 9, pigmentary epithelium ; 10, choroid (O'Day).

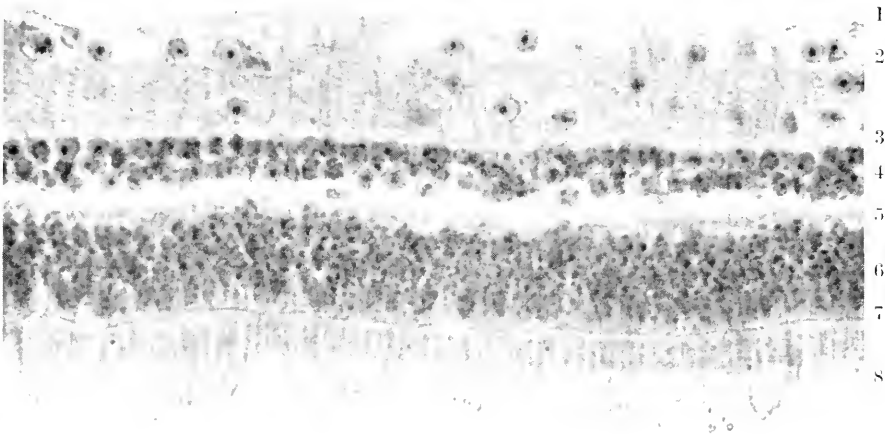


FIG. 546.—THE RETINA OF THE ECHIDNA.

1, optic nerve fibre layer ; 2, ganglion cells ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells (O'Day).

¹ p. 472.

the two epithelial layers and some radial blood vessels lying in loose connective tissue. The sphincter muscle, comprised of the unstriated fibres characteristic of Mammals, is massive ; it constitutes the only intra-ocular muscle for a dilatator or ciliary musculature is absent, nor is any accommodative mechanism present.¹

Except in the aquatic platypus, the *lens* is relatively small and flat and the zonular fibres, arising from the coronal zone of the ciliary body, are inserted into its equator. In this region the subcapsular epithelium is tall, twice as tall as at the anterior pole, to form a miniature annular pad, a characteristic of Reptiles (Fig. 543).

The *retina* is entirely avascular, dependent on the choroid for nutriment. Ophthalmoscopically the fundus of the echidna is of a

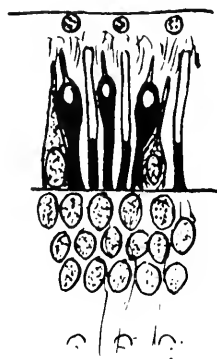


FIG. 547.—THE VISUAL ELEMENTS OF THE PLATYPUS.

Showing double and single cones (the latter in the centre) and the long slender rods (O'Day).



FIG. 548.—A VISUAL ELEMENT FROM THE PURE-ROD RETINA OF THE ECHIDNA (O'Day).

uniform brownish colour with a chalky-white oval optic disc from which nerve fibres radiate ; it thus closely resembles a common sauropsidan type (Johnson, 1901) (Plate XIII, Fig. 1). The visual elements are sauropsidan in character : the platypus has a duplex retina, the rods and cones being in approximately equal numbers. The cones are both single and double with oil-droplets in the former and in the chief member of the latter, but with no paraboloids ; the echidna has a pure-rod retina with no oil-droplets (Figs. 545 to 548). In neither genus is there evidence of an area centralis or a fovea. In the *optic nerves* of the platypus there are some 32,000 fibres (Bruesch and Arey, 1942).

THE OCULAR ADNEXA are sauropsidan apart from the extra-ocular muscles. The lids are thick and well-formed ; the echidna has a

¹ A dilatator is also absent in Crocodilians and Marsupials.

PLATE XIII
THE FUNDI OF MONOTREMES AND MARSUPIALS
(Lindsay Johnson)

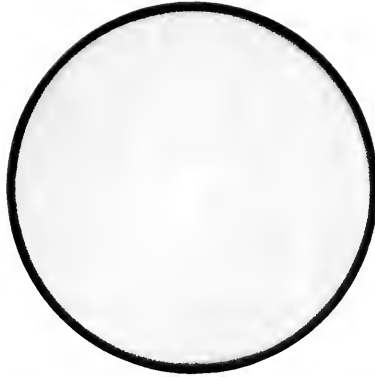


FIG. 1. —The Echidna.



FIG. 2.—The rufous rat-kangaroo,
Hypsiprymnus rufescens.

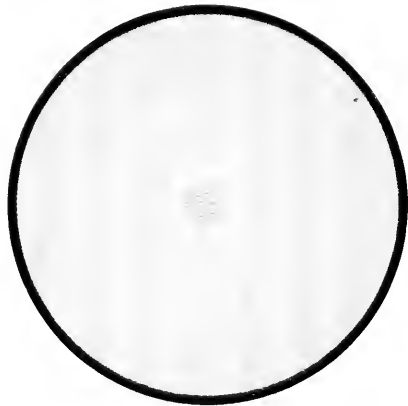


FIG. 3. —The squirrel-like phalanger,
Belidius sciurus.



FIG. 4. —The Virginian opossum,
Didelphus virginiana.



FIG. 5. —The Tasmanian devil, *Sarcophilus*
ursinus.

tarsus in the lower lid only ; the platypus in neither (Newell, 1953). Lacrimal and harderian glands are said to be present in both. The platypus has a well-formed and quite opaque nictitating membrane ; the ant-eater has none. The eye of the echidna, however, has a habit of rolling inwards and retracting into the socket rhythmically, an action aided by squeezing the lids (Johnson, 1901) ; the same protective phenomenon is seen in Edentates, the bandicoot and the porcupine. Both have the usual six extra-ocular muscles in addition to a retractor bulbi muscle ; but the superior oblique muscle is essentially mammalian in type. It will be remembered that in Vertebrates below Mammals the recti take origin from the apex of the orbit, the obliques from its anterior part¹; in Monotremes the superior oblique arises close to the origin of the recti and is threaded through a pulley in the supero-medial aspect of the anterior part of the orbit so that it runs sharply backwards towards the temporal aspect of the globe. This typically mammalian form is supplemented in the echidna by a second muscular slip running to the globe directly from the anterior nasal orbital wall, a relic of the sub-mammalian arrangement.

The orbit in the platypus is merely a shallow depression at the cephalic extremity of the combined temporo-orbital fossa, provided only with dorsal and median walls and without an interorbital septum—a non-mammalian configuration (Watson, 1916 ; Kesteven and Furst, 1929 ; de Beer and Fell, 1936). There is no optic foramen, for the optic and other cranial nerves leave the skull through a large pseudo-optic foramen (Watson, 1916 ; Hines, 1929).

THE MARSUPIAL EYE

The MARSUPIALS (METATHERIA)—in the Eocene period a large and widespread group—are today found only in Australasia with the exception of the American opossums (Didelphyidae),² arboreal, rat-like animals found in Central and South America, and the Selvas (Caenolestes), a primitive family until recently believed extinct, found in South America. In Australasia, however, where competition from the higher carnivorous Mammals has not occurred, there are many forms—(a) the cat-like dasyures (Dasyuridae) (including the squirrel-like banded ant-eater, *Myrmecobius*, and the Tasmanian devil, *Sarcophilus*); (b) the burrowing, mole-like Notoryctidae³ ; (c) the burrowing, rabbit- or rat-like bandicoots (Peramelidae) ; (d) the squirrel-like arboreal Phalangeridae, including the flying phalangiers, *Petaurus* and *Acrobates* (Phalangerinae), the bear-like wombats (Phascolomyinae), and the koala (Phascolarctinae) ; and (e) the unique kangaroos and wallabies (Macropodidae).



Banded ant-eater,
Myrmecobius



Marsupial mole,
Notoryctes

¹ p. 277, Fig. 293.

² Incidentally, among the American opossums, the pouch is generally absent, and the young are carried on the back of the mother, their tails coiled round hers.

³ *Notoryctes typhlops*, the marsupial mole, has vestigial eyes, less than 1 mm. in diameter, which lack lens, vitreous and visual cells, p. 733.



Spotted cuscus,
*Phalanger
maculatus*

The eyes of Marsupials represent a transition between the wholly reptilian-like eyes of Monotremes and the mammalian-like eyes of Placentals. The globe is spherical and the sclera fibrous like that of snakes, the ciliary musculature shows a reptilian ancestry but the structures accessory to reptilian accommodation have all been lost, the retina may have a vascularization either of the reptilian or mammalian type, a retinal tapetum as occurs in some Reptiles may be present, and the visual elements, closely resembling those of Monotremes, are typically reptilian.



FIG. 549.—THE EYE OF THE WALLABY ($\times 5$) (O'Day).



Dasyure,
Dasyurus

THE GLOBE OF THE EYE is spherical or almost spherical, with a large cornea and a fibrous sclera without cartilaginous or osseous supports; the marsupial mole, *Notoryctes*, has cartilaginous nodules in the sclera. There is no Bowman's membrane but a thick Descemet's membrane. The choroid is of the mammalian type with, in a few species, a tapetum fibrosum (the flying phalanger, *Petaurus*, and some of the Dasyuridae—the cat-like *Dasyurus*, the Tasmanian wolf, *Thylacinus*, the Tasmanian devil, *Sarcophilus*). In *Dasyurus* this extends over the entire fundus but is functional only in the upper half where the retinal epithelium is devoid of pigment. The ciliary body is well formed and provided with processes, and a ciliary musculature is always present despite the fact that no accommodation has yet been demonstrated in any member of the group (Figs. 550–1). Sometimes the muscles are disposed as in Reptiles, comprised of a meridional muscle (of



Tasmanian devil,
Sarcophilus

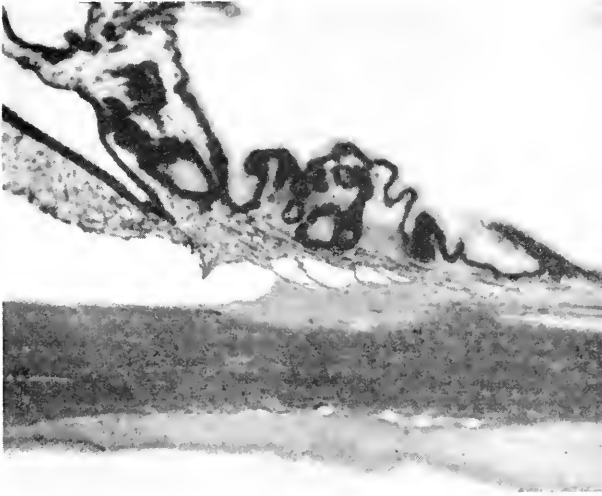


FIG. 550.—THE CILIARY REGION OF THE WALLABY.

Showing the well-formed ciliary processes, the meridional muscle, and the well-formed fibres of the pectinate ligament traversing the deep ciliary cleft ($\times 60$) (O'Day).

Brücke) arising from the cornea; more often circular fibres are added anteriorly (*Dasyurus*; the opossums, *Marmosa*, *Didelphys*, etc.). The iris is densely pigmented and richly vascularized with many vessels standing out from the anterior surface; the pupil is round (in *Dasyurus viverrinus* the contracted pupil is a vertical slit) and a sphincter of unstriated muscle surrounds the pupillary margin but a dilatator is absent. In the bandicoot, *Perameles*, nipple-like cystic protrusions of the pigmented retinal layers form flocculi¹ around the pupillary margin. The angle of the anterior chamber and the circumferential ciliary venous sinus are of the mammalian type (Fig. 550).

The lens is comparatively large, flat in diurnal, round and almost filling the interior of the globe in the smaller nocturnal types; there are often traces of the annular pad of Reptiles, but it never touches the ciliary processes as is characteristic of Sauropsida.

The type of retinal vascularization varies. Usually this structure is avascular, and, as if in compensation, the choroidal vessels are so large as to be easily seen ophthalmoscopically (except in some phalangers); frequently there

¹ p. 469.



Opossum,
Didelphys



FIG. 551.—THE CILIARY PROCESSES OF THE KANGAROO, *MACROPUS AGILIS* (after Franz, 1911).

I, iris; CS, ciliary shelf.



Wallaby,
Petrogale

are fine vessels on the optic disc, sometimes (as in the kangaroo and wallaby) projecting like a dome-shaped cushion above it resembling a vestigial reptilian cone.¹ In those species, however, wherein the choroid is under-developed (the flying-phalanger, *Petaurus*) or is insulated from the retina by an impermeable retinal tapetum, a mammalian-like retinal circulation exists, paired arteries and veins radiating from the disc in the inner layers of the retina, clothed in glial sheaths and protruding somewhat into the vitreous; in the opossum, *Didelphys*, the capillaries penetrate through the entire thickness of the retina to the external limiting membrane (Plate XIII).

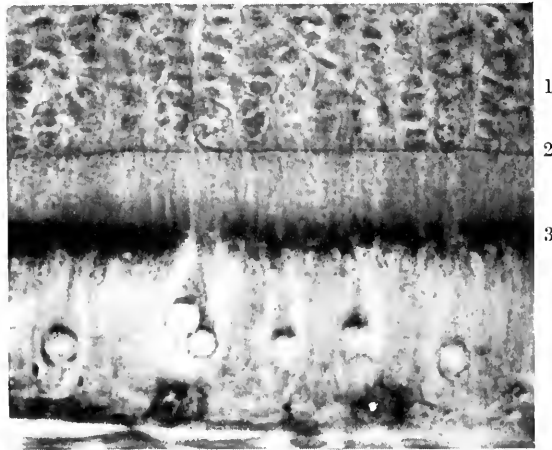


FIG. 552.—THE VISUAL CELLS OF AN AUSTRALIAN MARSUPIAL.

The native cat, *Dasyurus viverrinus*. 1, outer nuclear layer; 2, external limiting membrane; 3, visual cells, showing the filamentous rods and the single and double cones with oil-droplets (in both members of the latter) (O'Day).



Koala,
Phascolarctus

In the Virginian opossum, *Didelphys virginiana*, a retinal tapetum exists, a unique phenomenon among Mammals apart from the fruit-bat, *Pteropus*. The tapetum is in the form of a semi-circle with its straight horizontal lower edge at the level of the disc; in this area the epithelial cells are tall, devoid of pigment and packed with guanine-like crystals of unknown chemical nature. The visual cells are reptilian in type and resemble those of the monotreme eye (O'Day, 1936-39); the retina, in fact, is that of a Sauropsidan in the eye of a Mammal (Figs. 552-3). The rods are filamentous and outnumber the cones which are either single or double in type, lacking paraboloids but possessing oil-droplets. It is interesting that in all Australasian types so far examined double cones have oil-droplets in both members; this is a rare

¹ p. 362. Compare also the Rodents, p. 481.

condition which occurs only exceptionally in American Marsupials and it is noteworthy that in American opossums some of the single cones lack oil-droplets. It is also interesting that among Mammals only the Monotremes and Marsupials have either double cones or oil-droplets.



Wombat,
Phascolomys

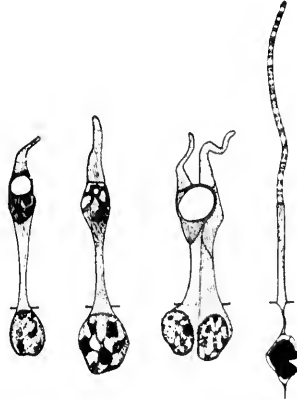


FIG. 553.—THE VISUAL CELLS OF AN AMERICAN MARSUPIAL.

The American mouse-opossum, *Marmosa mexicana*, showing (from left to right) a single cone with oil-droplet, a single cone without oil-droplet, a double cone with an oil-droplet in one member, and a long filamentous rod ($\times 1,000$) (Gordon Walls).

THE OCULAR ADNEXA have received little attention. A poorly developed nictitating membrane is present, a harderian and a lacrimal gland as well as a retractor bulbi muscle. The Virginian opossum, *Didelphys virginiana*, has no true nictitating membrane; two folds of conjunctival tissue arising from either canthus close over the eye in the mid-line while the globe retracts into the socket. In other forms (the bandicoot, *Perameles*) when the eye is touched the globe rolls backwards and retracts as the nictitating membrane flashes over it, the lids sometimes closing over it at the same time.



Rabbit bandicoot,
Peragale

THE PLACENTAL EYE

The PLACENTALS (EUTHERIA) comprise the vast majority of Mammals and include a multitude of types. These can be arranged in 15 orders, the enumeration of which will facilitate understanding of the subsequent discussion.

(1) INSECTIVORA, the most primitive type of Placentals found widely in temperate and tropical lands except S. America and Australasia (where insectivorous opossums exist).

The most widely known representatives are the true shrews (Soricidæ), the true moles with vestigial eyes (Talpidæ) including the water-moles or desmans (*Myogale*), and the hedgehogs (Erinaceidæ). Further types are the otter-shrew of W. Africa (*Potamogale*), the oriental tree-shrews (Tupaiidæ) (sometimes classed among the Prosimians), the elephant-shrews (Macroscelidæ) of Africa with very

TYPICAL MAMMALS : 1

(Drawn not to scale but to a standard size)

INSECTIVORA



Hedgehog



Golden mole



Tree-shrew

CHIROPTERA



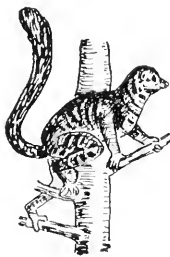
Flying fox

DERMOPTERA



Flying lemur

PRIMATES



Lemur



Tarsier

" EDENTATA "



Armadillo



Pangolin



Aard-vark

RODENTIA



Marsh



Beaver



Porcupine



Vizcachas

large eyes, and the golden mole of S. Africa (*Chrysochloris*), the eyes of which are small and hidden under the skin. There are two further and little known representatives extant—the tenrees of Madagascar and *Solenodon* of Cuba and Haiti. Most are terrestrial, some are burrowers, some (the tree-shrews) arboreal, and a few aquatic (*Myogale*, *Potamogale*). Most feed on insects; some arboreal forms eat leaves as well; the moles eat worms; and the otter-types, fish.

From the Insectivora three orders are directly derived—the Chiroptera, the Dermoptera and the Primates.

(2) CHIROPTERA (bats), the only Placentals capable of active flight; the arms and the fingers, with the exception of the first, the hindlegs and (in the Microchiroptera) the tail, support a fold of skin which constitutes the wing.

Two sub-orders exist: (1) the large MEGACHIROPTERA—the huge flying foxes of Africa and the Pacific countries (*Pteropus*) with a wing-span of up to 5 feet and large eyes (Fig. 750), the giant bats of India (*Cynopterus*) and of the Egyptian pyramids (*Xantharpyia*); and (2) the small insectivorous MICROCHIROPTERA found all over the world—the British *Eptesilio*, the American blood-sucking vampire, *Desmodus*, etc.

(3) DERMOPTERA (flying lemurs), arboreal vegetarians which glide from tree to tree buoyed up by a fold of hairy skin connecting the fore and hind limbs. They inhabit Malaya and the Philippines (*Galeopithecus*).

(4) PRIMATES. An order derived from the primitive Insectivores; they were primarily and still mainly remain arboreal. They comprise three sub-orders: the Lemuroidea, the Tarsioidea and the Anthropeidea, the first being the most primitive and the last the most advanced; the first two are frequently known as Prosimians, the last constitutes the Simians.

(a) LEMUROIDEA, small nocturnal lemurs of Ethiopia and the East, have many primitive characters in common with the Tupaiidae with which they seem to have had a common origin. They fall into two groups—true lemurs (Lemuridae) confined to the island of Madagascar, and the Lorisidae, never found in Madagascar—*Loris* and *Nycticebus* of the E. Indies, the potto, *Perodicticus* (Fig. 752), and the agwantibo, *Arctocebus*, of W. Africa, and the bush-baby, *Galago*, of Africa.

(b) TARSIOIDEA, of which there is only one survivor, the tarsier (*Tarsius*), differ from the lemurs among other things in having the orbit directed forwards and almost completely separated from the temporal fossa. They are generally looked upon as a separate line of evolution which branched off the Primate stock at an early period and eventually produced the Anthropoids.

(c) ANTHROPEIDEA, comprising 5 families of essentially diurnal species, distributed between the New World (Platyrrhini) and the Old (Catarrhini):

- (i) HAPALIDÆ—marmosets—the most primitive monkeys, small squirrel-like creatures, found in C. and S. America;
- (ii) CEBIDÆ—the American monkeys—including such species as the capuchins (*Cebus*) imported into Europe; *Nyctipithecus* (*Aotes*), the only nocturnal monkey; the bald-headed sakis (*Pithecia*); the long-limbed spider monkeys (*Ateles*); and the howling monkeys (*Alouatta*);
- (iii) CERCOPITHECIDÆ—the Old World monkeys, including the African baboon (*Papio*), the mandrill (*Mandrillus*), the macaques (*Macaca*), etc.;
- (iv) SIMIIDÆ—the anthropoid apes, including the gibbon (*Hylobates*), the orang-utan (*Pongo*), the chimpanzee (*Pan*), and the gorilla (*Gorilla*);

TYPICAL MAMMALS : II
(Drawn not to scale but to a standard size)

CARNIVORA



Lynx



Hyæna



Raccoon



Coati



Civet cat



Polecat



Badger



Sea-lion

ARTIODACTYLA



Llama



Gazelle



Giraffe



Chevrotain

PERISSODACTYLA



Zebra



Rhinoceros



Tapir

HYRACOIDEA



Hyrax

CETACEA



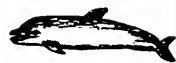
Blue



Hump-back whale



Sperm whale



Dolphin

- (v) HOMINIDÆ, with several extinct genera (*Pithecanthropus*, etc.) and the single living genus, *Homo*.

(5) XENARTHRA—these comprise three distinct sub-orders :

(a) the solitary nocturnal, arboreal sloths (BRADYPODIDÆ) (3-toed *Bradypus*, or 2-toed *Choloepus*) of S. and Central America, vegetarian in habit, which spend a sluggish life hanging from the branches of trees (Fig. 751) ;

(b) the terrestrial or arboreal ant-eaters (MYRMECOPHAGIDÆ) of neo-tropical distribution ;

(c) the omnivorous nocturnal armadillos (DASYPODIDÆ), mainly of S. America, with a dermal armature of bony scutes, which actively run and burrow.

(6) PHOLIDOTA. The small family of burrowing, termite-eating, scaly pangolins (*Manis*) of Ethiopia and the East.

(7) TUBULIDENTATA. The equally small family of shy, nocturnal, termite-eating aard-varks (*Orycteropus*) of Africa, living in burrows.

The Xenarthra, Pholidota and Tubulidentata used to be classed together as EDENTATA owing to the simplicity of their teeth or the lack of them.

(8) RODENTIA, the largest order of Mammals, comprising more than 4,000 species, mainly small, terrestrial and vegetarian, which gnaw their food in a characteristic way. They are represented by two sub-orders¹ according to their dentition :

(a) those provided with two pairs of upper incisors (LAGOMORPHA)—the rabbit (*Oryctolagus*), the hare (*Lepus*) and the pikas or calling hares (*Ochotona*) ;

(b) those provided with a single pair of upper incisors, which are conveniently divided into three groups :

(i) the SCIUROMORPHA—the common squirrel (*Sciurus*), the souslik or ground squirrel (*Citellus*), the prairie-dog (*Cynomys*), the flying squirrel (*Pteromys*), the marmot (*Marmota*), the beaver (*Castor*) ;

(ii) the MYOMORPHA—the rat (*Rattus*), the mouse (*Mus*), the vole (*Microtus*) ;

(iii) the HYSTRICOMORPHA—the porcupine (*Hystrix*), the guinea-pig (*Cavia*), the chinchilla, the vizcacha (*Lagostomus*), the coypu (*Myocastor*), and others.

(9) CARNIVORA. A large amorphous order of active and fierce flesh-eaters of wide distribution and mostly terrestrial. It is comprised of 2 sub-orders :

(a) the terrestrial FISSIPEDIA, including 7 families : the cat-like Felidæ (cat, lion, tiger, leopard, cheetah, jaguar, lynx), the Viverridæ (civet cats, mongoose, etc.), the Hyænidæ (hyænas), the dog-like Canidæ (dog, wolf, jackal, fox, etc.), the bear-like Ursidæ, the Procyonidæ (Himalayan pandas, and the American raccoon and coati), and the Mustelidæ (otter, sea-otter, skunk, badger, marten, polecat, ferret and weasel, etc.) ;

(b) the aquatic PINNIPEDIA, marine fish-eating Carnivores, clumsy on land where they come for breeding purposes : Phocidæ (seals), Otariidæ (sea-lions or eared-seals), and Odobænidæ (walruses).

(10) ARTIODACTYLA. Even-toed hoofed animals, terrestrial and herbivorous in habit, wherein the hoof is formed by the third and fourth digits showing a cleft between. Of these there are four extant groups :

(a) the SUOIDEA (pigs and boars, Suidæ ; peccaries of America, Dicotylidæ ; and the African hippopotamus) ;

¹ The Lagomorpha are now generally accepted as a separate order.

(b) the TYLOPODA (camel and dromedary of Africa and Asia, and the llama of S. America) ;

(c) the PECORA (Ruminants) (deer and giraffe, and the Bovidae—ox, bison, sheep, goat, antelope, gazelle) ;

(d) the TRAGULINA, small chevrotains of the East and Africa.

(11) PERISSODACTYLA. Odd-toed hoofed animals wherein the foot is essentially formed by the enlarged third digit—Equidae (horse, ass, zebra), Rhinocerotidae (rhinoceros), Tapiridae (tapir).

(12) HYRACOIDEA, the small rodent-like hyraxes (" coneys ") of Africa and Syria of arboreal habits.

(13) PROBOSCIDEA, the vegetarian elephants of Africa (*Loxodonta africana*) and the Orient (*Elephas maximus*).

The Artiodactyla, Perissodactyla, Hyracoidea, and the Proboscidea used conveniently to be classed in one heterogeneous group of UNGULATA (hoofed animals).

(14) SIRENIA.¹ The sluggish, vegetarian, and fully aquatic fish-like sea-cows, which crop grasses in shallow littoral waters—the manatee (*Manatus* ; *Trichechus*) of S. America and S. Africa, and the dugong (*Halicore*) of Oriental and Australian coasts.

(15) CETACEA. The carnivorous fish-like whales and dolphins, fully adapted for marine life. There are two distinct orders :

(a) the baleen whales (MYSTACOCETI) with baleen (or whale-bone) plates instead of teeth, which sound to great depths and feed blindly by trawling for plankton which they strain through the frayed margins of their plates (the right-whale, *Balæna* ; the hump-back, *Megaptera* ; the blue whale or rorqual, *Balenoptera*, etc.) ; the great rorquals (particularly the blue whale) are the largest animals in existence, over 100 feet in length and well over 100 tons in weight ;

(b) the toothed whales (ODONTOCETI), squid- and fish-eating animals which use their vision to catch their prey and are therefore adapted with more perfect eyes, some of them swimming in packs like wolves attacking the unwieldy whale-bone whales (the sperm-whale, *Physeter* ; the killer whale, *Orcæ* ; the narwhal, *Monodon* ; the porpoise, *Phocæna* ; the dolphin, *Delphinus*). There is a small family of fresh-water dolphins (the susu, *Platanista*) with rudimentary eyes.

Within the many orders of Placentals a considerable range of variations in the structure of the eye occurs, but throughout the entire class the similarity is great. It seems likely that the first representatives (Insectivora) were nocturnal in habit, and that, as occurs in snakes, the eye has evolved from this as a basis showing innumerable adaptive changes to suit the many environments (diurnal, arboreal, aquatic, etc.) to which the prolific class has suited itself. Only in a few instances among the Insectivores (moles) and Rodents has the burrowing habit led to the degeneration of the eyes.² The general characteristics of the placental eye may be summarized as follows (Figs. 554 to 563).

¹ The legend of the mermaid is said to derive from sailors' fanciful descriptions of the manatee sitting on the rocks nursing its baby in its arms ; hence the generic name, Sirenia. It is to be remembered that a third species, *Rhytina* (Steller's sea-cow), growing to enormous dimensions (25 feet or more), was found in great herds by Berin in 1741 near the Asiatic coasts of the Bering sea. Sluggish and docile in habit it became extinct at the end of the 18th century owing to its wholesale massacre for food.

² Figs. 554, 555, 556, 557, 558, 559, 560, 561, 562, 563.

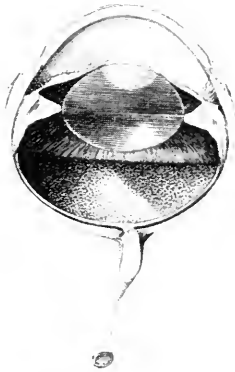


FIG. 554.—The lynx,
Felis lynx.

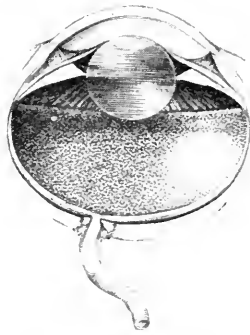


FIG. 555.—The seal,
Phoca grænländica.

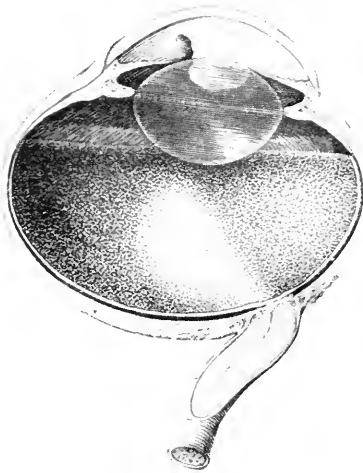


FIG. 557.—The horse,
Equus caballus. Note
the flocculus in the
pupil.



FIG. 556.—The marmot,
Marmota alpina.



FIG. 558.—The porcupine,
Hystrix cristata.

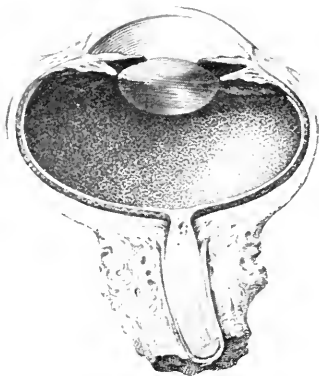


FIG. 560.—The elephant,
Elephas maximus.



FIG. 559.—The wolf,
Canis lupus.



FIG. 561.—The monkey,
Simia inuus.

A selection of Soemmerring's engravings illustrating in natural size the lower half of the hemisected left eye in each case.

The lack of any scleral support, cartilaginous or bony, results in a spherical globe.

The choroid is of the standard vertebrate type, usually thinner than that of man, and may contain a tapetum. The ciliary body has a variable topography, but the ciliary muscle, often vestigial, is always composed of plain muscle fibres. A peculiarity is that the anterior surface of the iris is partially covered by a mesodermal leaf additional to that found in other Vertebrates. The angle of the anterior chamber is continued by a cleft of varying depth, extending into the ciliary region bridged across by delicate strands of uveal tissue.

The lens—usually lenticular in shape but round in aquatic species—is suspended freely from the ciliary processes by a well-developed zonule and is deformed in accommodation (when this function is present) by the elasticity of its capsule, being stretched or relaxed by the ciliary muscle.

The retina with few exceptions is duplex in type and of typical vertebrate architecture.

Most of these characteristics are seen in some form or another in other classes of Vertebrates : in only three features does the placental eye differ characteristically from all others :—

1. In the development and fate of the hyaloid system of vessels, the persisting remnants of which frequently supply an intra-retinal system of vascularization.
2. In the formation of a mesodermal layer of the iris superficial to the structures found in other Vertebrates.
3. In an accommodative mechanism depending on a relaxation of the tension normally maintained upon the capsule of the lens.

It is unnecessary in a volume of this type to describe the detailed morphology of the placental eye which conforms closely with that of man—to which an entire subsequent volume will be devoted. It will suffice to describe those features which show marked variations from the general scheme (Figs. 554 to 563).

The General Shape and Size of the Globe. In shape the placental eye is spherical, a necessity with its fibrous, unbuttressed sclera. As a rule the cornea continues the scleral curve, although sometimes there is a shallow corneo-scleral furrow with a protruding cornea having a smaller radius of curvature, as in man ; alternatively, while the peripheral zone of the cornea maintains the curve of the sclera, its apex may be more acutely curved, as is seen in Carnivores. In Cetaceans the shape of the globe is fish-like¹ with a short antero-posterior axis ; it is interesting that the Pinnipedes, less wholly adapted to an aquatic existence than the Cetaceans, have a spherical globe. In some nocturnal prosimian Primates such as the lemuroids (*galago* and *Myocebus*) and *Tarsius* the shape is almost tubular (Fig. 743).

¹ p. 276.

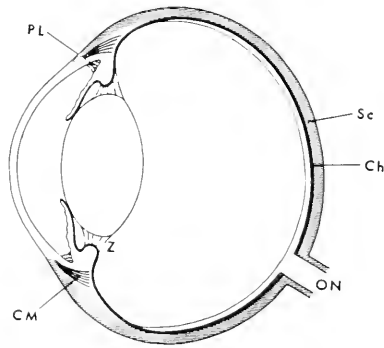


FIG. 562.—DIAGRAM OF THE EYE OF A PLACENTAL.

Ch, choroid ; CM, ciliary muscle ; ON, optic nerve ; PL, pectinate ligament bridging the ciliary cleft ; Sc, sclera ; Z, zonule. Note the relative simplicity of the eye.



FIG. 563.—SECTION OF THE EYE OF THE CAT ($\times 3.25$) (Norman Ashton).

The size of the globe varies within wide limits ; neglecting the minute degenerate eyes of the mole (0.8 mm. diam.) and one or two species of burrowing rodents,¹ it ranges from 1 to 2 mm. in diam. in the shrews and bats to the enormous eyes of some whales (145 \times 129 \times 107 mm. in the great blue whale, *Balenoptera musculus*) (Pütter, 1903). In comparison with the size of the body, however, that of the eye is more uniform : while the former varies as 1 : 60 among terrestrial Placentals, the latter only varies as 1 : 30. The eye of the seal (internal antero-posterior diam., 52 mm.) is comparatively

¹ p. 733.

much larger than that of the whale, which, in fact, measures only 1/250 to 1/600th of its gigantic body (Figs. 555, 564); that of the elephant (axis 35 mm.) or rhinoceros (axis 23 mm.) is correspondingly small (Fig. 560), and the minute eye of the vole (axis 1.75 mm.) is relatively greater in comparison with the length of its body (10 cm.) than is the eye of man. Although as a general rule Haller's ratio¹—that the size of the eye varies inversely as the size of the body²—holds good, marked variations occur with the visual habits of the animal. In the lower orders of nocturnal habits which depend little on vision (Insectivores, Chiroptera, Edentates and some Rodents) the eyes are small relatively and absolutely; in the more highly developed and visually alive types they are larger. Among these it varies generally with the visual efficiency and swiftness of movement, and is generally larger in nocturnal species. Thus the eye of the nimble horse (axis 45 mm.) is larger than that of the lethargic elephant (axis 35 mm.) (Fig. 557), while the small (usually nocturnal) Primates have comparatively larger eyes than the large diurnal species (with the conspicuous exception of the Hapalidæ—marmosets and tamarins) (Ashley-Montague, 1943–44) (Figs. 752 and 753).

Measurements of the various placental eyes are found in Emmert (1886), Pütter (1903), Hotta (1906), Kolmer (1910), Franz (1912), Linsenmeyer (1912), Guist (1923), Wolfrum (1926), Rochon-Duvigneaud (1943) and Steindorff (1947); their weight and volume in Liebig (1874), Koschel (1883), Emmert (1886), Welcker (1903), Schleich (1922), Vitello (1931), Steindorff (1947) and Henderson (1950).

The *corneo-scleral envelope* corresponds with that of man with the exception of the aquatic Placentals, apart from the generalization that the eye of a relatively large animal tends to have an unusually thick sclera—elephant, rhinoceros, etc. The envelope is entirely fibrous without any supporting skeletal structures.³ Among the Cetaceans particularly the sclera is enormously thick, a feature described by Bennett (1836); indeed, the sclera at the posterior pole may be 3/4 the length

¹ p. 401.

² Magnitudo oculorum est fere in ratione inversa animalium. Balæne, Rhinoceroti, Elephanto parvi sunt oculi. Haller, *Et. Phys.* IV–XVI (1768).

³ A FIBROUS SCLERA is also found in Cyclostomes, pearl-fishes and some eels, adult Urodeles (excluding *Triton* and *Hynobius*, and degenerative limicoline types), some tree frogs, snakes and Marsupials (excluding *Notoryctes*).

CARTILAGE is found (a) in the form of a posterior cup in Fishes (except Teleosteans), adult Amurans (except some tree frogs), larval Urodeles, Reptiles (excluding snakes and the chameleon), Birds and Monotremes; (b) in the form of a ring in Teleosteans; (c) as islands in elephant fishes, *Triton* and *Hynobius*, limicoline Urodeles (enormously large), the chameleon (at the fovea) and *Notoryctes*; (d) calcified in some Selachians and some Teleosteans.

OSSE is found (a) as anterior ossicles in most Teleosts, Chondrosteans, Cœlacanth, Reptiles (excluding snakes and Crocodilians) and Birds; (b) in the form of a ring in *Xiphias* and *Thunnus* (anteriorly), *Hypopachus*, and many Birds (posteriorly as the os opt.

of the antero-posterior axis of the globe. In the hump-back whale, *Megaptera*, for example, the antero-posterior diameter of the eye is 40 mm., the thickness of the sclera at the posterior pole is 30 mm., while its thickness at the limbus is only 3 mm. (Rochon-Duvigneaud, 1943) (Fig. 564). The cornea of this species is correspondingly thin (1.5 mm. at the periphery ; 0.5 mm. at the apex). In addition, the whale has an immensely thickened accessory optic nerve sheath composed of connective-fatty tissue lying outside the dural sheath

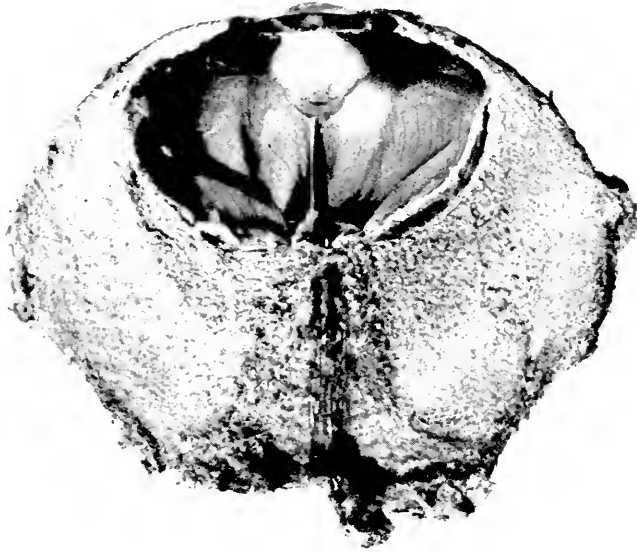


FIG. 564.—THE EYE OF THE WHALE.

A hemisection to show the enormous thickening of the sclera and the accessory optic nerve sheath. Note that the relatively small lens is kept in place artificially by a glass strut (specimen from A. Arruga : Museum, Institute of Ophthalmology).

encased in a thick aponeurotic-like capsule. Set on this massive stalk, the globe, of course, is immobile. A similarly thick accessory sheath surrounds the optic nerve of the elephant and the hippopotamus (Rochon-Duvigneaud, 1943) : in both of these the sclera is very thick and the eyes are capable of little movement.

The phenomenal thickness of the sclera in the whale is often said to be necessary to resist the enormous pressures involved when the animal sounds to great depths. It is to be remembered, however, that the cornea is thin and that abyssal fish do not share this characteristic ; the sclera of the deeply diving shark, *Etmopterus*, is microscopically thin and that of the *Chimæras* discontinuous.¹ It is probable, indeed, that reinforcement in this sense is un-

¹ p. 290.

FIGS. 565 TO 572.—THE CORNEAL EPITHELIUM OF MAMMALS.

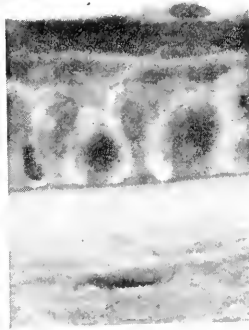


FIG. 565.—Rabbit.

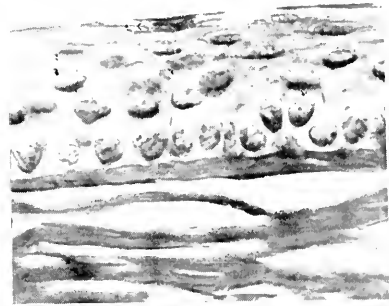


FIG. 566.—Dog.



FIG. 567.—Guinea-pig.

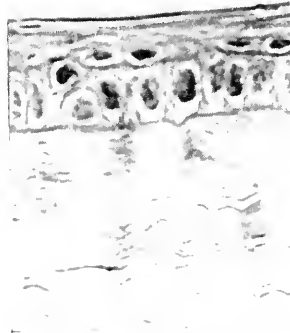


FIG. 568.—Rat.

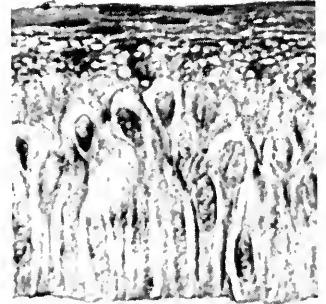


FIG. 569.—Pig.

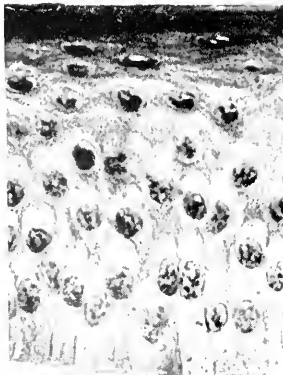


FIG. 570.—Horse.

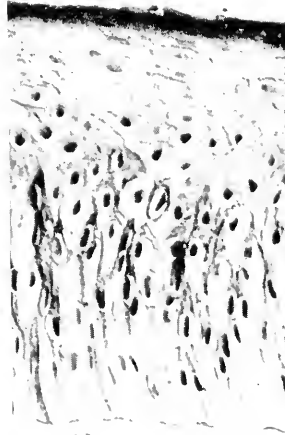


FIG. 571.—Ass.

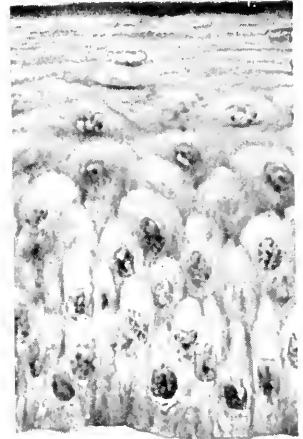


FIG. 572.—Ox.

565.—Periodic acid Schiff's stain (Norman Ashton).

566 to 572.—Masson's trichrome stain (Cahnettes, Déodat, Planel and Bee).

necessary for the pressure on the surface is equally transmitted to all the fluid contents of the body including the inner eye. It is more likely that the reinforcement of the posterior region of the sclera is necessary to maintain the non-spherical shape in the huge cetacean globe rendered mechanically weak by its great size, thus taking over the supportive function of the scleral cartilage in fishes with similarly shaped eyes.

The *cornea* of Placentals is usually circular or almost so, but in Cetaceans and in a great number of the Ungulates (Equidæ, Ruminants and the hippopotamus) it is horizontally oval corresponding to the configuration of the pupil. In many, a pigmented ring encircles the limbus spreading a considerable distance into the corneal tissue ; sometimes this is confined to epidermal pigment (Rodents such as rabbit, hare, guinea-pig, rat, marmot, etc. ; the horse and the gorilla) (Fig. 697) ; sometimes to this is added pigment in the deep interstitial tissues (Carnivores such as the cat, dog, fox, lion ; Ruminants such as

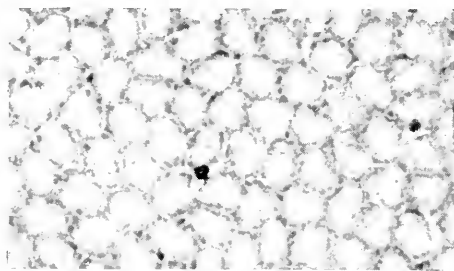


FIG. 573.—THE ENDOTHELIUM OF THE CORNEA OF THE RABBIT.

Showing a sheet of corneal endothelium lining the anterior chamber which has been stripped away from Descemet's membrane. No nerve fibres are seen but there are a few circular blobs of stain lying between the cells ($\times 400$) (Zaunders and Weddell).

the ox and deer ; the porpoise, the dolphin, the whale and the chimpanzee). In the rhinoceros the pigmented region of the cornea is vascularized. The pigmentation may be an anti-glare device for it is absent in crepuscular or nocturnal animals.

The histological structure of the cornea is built on the typical vertebrate plan seen in man except that most species have no Bowman's membrane ; Descemet's membrane with its endothelium, however, is always present and is often very substantial. Although Bowman's membrane is a relative rarity, the basal membrane of the epithelium seems always to be present (Calmettes *et al.*, 1956 ; Sheldon, 1956). The thickness of the epithelium varies considerably (Figs. 565 to 572)¹ ; that of the endothelium is constant (Fig. 573). Blood vessels sometimes invade the cornea proper from the limbus, whereas in Primates

¹ 20 layers of cells in the horse ; 10-12, pig ; 9-11, ox ; 8-10, dog ; 6-8, rabbit ; 5-6, guinea-pig, rat (Virchow, 1910 ; Calmettes *et al.*, 1956).



FIG. 574.—A diagrammatic representation of the arrangement of the nerve bundles which enter the periphery of the cornea in different planes (methylene blue).

Upper left quadrant: the nerve bundles entering the cornea from the episcleral plane. Upper right quadrant: entering from the subconjunctival plane. The lower half shows the manner in which the plexiform pattern of nerve fibres arises from these bundles. It is to be noted that they are not by any means all radially disposed and that some fibres pass from limbus to limbus across the centre of the cornea.



FIG. 575.

FIG. 575.—Terminals in the substantia propria arising from a nerve bundle (methylene blue) ($\times 350$).

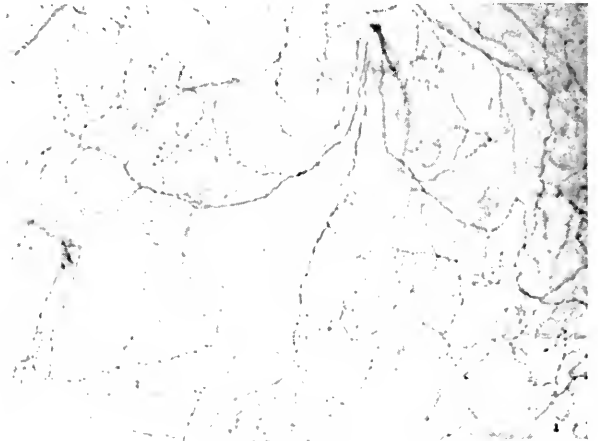


FIG. 576.

FIG. 576.—Nerve terminals in the epithelium showing the axons piercing Bowman's membrane, multiplying and passing in all directions in the epithelium. The stromal plexus is out of focus (methylene blue) ($\times 130$).

they are found only in foetal life ; in some animals they persist much longer (*e.g.*, cat), while in others they may be permanent (ox, sheep, Gerlach, 1848). In most Mammals the nerve plexus is more complicated than in man.

Since the early observations of Schlemm (1831) who demonstrated nerve-fibres entering the cornea in stags and oxen, a considerable amount of work has been done on this problem. Most of the early work¹ is unconvincing, but Cohnheim (1866-67), by introducing the gold chloride impregnation technique, demonstrated their presence and complexity in the cornea of rabbits and guinea-pigs, as well as in frogs and birds. This advance was followed by a large number

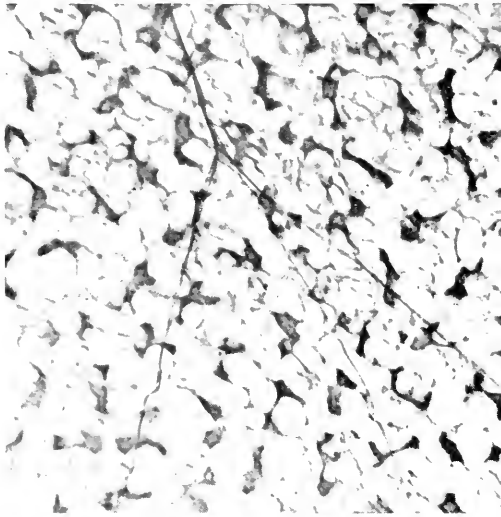


FIG. 577.—THE NERVES IN THE CORNEAL ENDOTHELIUM IN THE RABBIT.

Flat section, fixed in bromformalin, stained with del Rio Hortega's "panoptic silver carbonate technique" (J. R. Wolter).

of contributions which were assessed in the important papers of Waldeyer and Izquierdo (1880) and Ranvier (1881) wherein the innervation of the cornea of Fish, Amphibians, Reptiles and Birds as well as Mammals was assessed. The introduction of the methylene blue method of staining nerve fibres stimulated a classical paper by Dogiel (1891) dealing with the monkey and man, while a considerable number of Mammals was studied using the silver technique by Crevatin (1903), Bielschowsky and Pollak (1904) and Cajal (1909). This work was consolidated chiefly on Mammals by Virchow (1910), Agababow (1912) and particularly Attias (1912). More recent studies using a variety of techniques including polarization and phase-contrast microscopy are those of Boeke and Heringa (1924) (monkey), Nakajima (1930) (rabbit), Egorow (1934) (guinea-pig), Boeke (1935) (monkey), Reiser (1935-37) (pig and guinea-pig), Borr (1939) (rat), Peris (1947-49) (bull, sheep, rabbit, pig, cat, etc.), Rodger (1950)

¹ Bochdalek (1837-39) (larger Mammals), Pappenheim (1839-40) (oxen), Purkinje (1845) (different Mammals), Köl liker (1848-66) (rabbits), Luschka (1850) (rabbits), Ciaccio (1863-81) (mice).

(rabbit), Zander and Weddell (1951) (rat, guinea-pig, rabbit, monkey and man, as well as the dogfish, *Scyllium*, and the frog, *Rana*), Rexed and Rexed (1951) (rabbit), Itahashi (1952) (rabbit), Bell *et al.* (1952) (cat), Palumbi (1953) (rabbit, rat, cow, horse, and man), and Wolter (1955-56) (rabbit).

Branches of the ciliary nerves derived from the ophthalmic division of the trigeminal enter the cornea at the limbus. After supplying a perilimbal plexus, they lose their myelin sheaths and run radially into the corneal stroma in some 70 to 80 nerve-trunks (Fig. 574). As these branch they form a plexiform arrangement at all levels in the stroma, more dense, however, in the superficial layers. Some of the branches terminate in the stroma in bead-like thickenings (Fig. 575); many of them terminate in the corneal epithelium penetrating Bowman's membrane when this structure is present. In this layer the nerve fibres shed their sheaths of Schwann and the naked axons subdivide to form a delicate

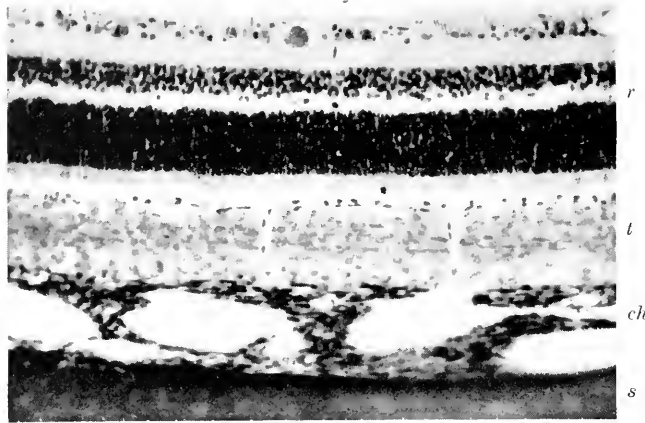


FIG. 578.—THE POSTERIOR SEGMENT OF THE EYE OF THE KITTEN.
ch, pigmented vascular choroid; *r*, retina; *s*, fibrous sclera; *t*, tapetum
 ($\times 150$) (Norman Ashton).

plexus terminating in beaded formations in all layers of the epithelium. Although there appear to be histological differences between the fibres, the evidence suggests that these nerves are all of a sensory nature (Fig. 576).

A most interesting finding has been reported by Wolter (1957)—the presence of nerve fibres in the endothelium of the cornea in the rabbit (Fig. 577); their function is unknown, nor have they been observed in other Vertebrates.

An interesting peculiarity is the *keratinization of the corneal epithelium* seen in two types of Placentals. In some aquatic forms (seals, dolphins and particularly in whales) the epithelium is thick and keratinized as a protection against sea-water¹; while in the ant-eating Placentals (Xenarthra, as the armadillo; Tubulidentata such as the aard-vark) a similar keratinization occurs, corresponding to that seen in the ant-eating Monotremes (the echidna), presumably a protection against the formic acid emitted in defence by the termites. The armadillo, *Dasypus*, is peculiar in that the cornea is vascularized to its apex, probably a necessary source of nutriment since the heavily cornified epithelium

¹ Compare the thick corneal epithelium of the platypus, *Ornithorhynchus* (p. 433).

is impervious to tears and presumably cannot mediate an adequate respiratory exchange.

The Choroid. The layers of the choroid in the placental eye correspond with those of man (Fig. 578).¹ the choriocapillaris being usually thin, exceptionally so in the Sciuridæ (squirrels) and Gliridæ (dormice) : exceptions to this are aquatic types (Pinnipedes, Cetaceans) wherein the choroid is unusually thick. One interesting and variable feature, however, is the TAPETUM LUCIDUM,² an adaptation acquired by certain nocturnal animals to improve vision in dim illumination. Optically the tapetum acts as a mirror which, lying behind the rods and cones, reflects the incident light so that it traverses the visual elements twice, thus increasing differences in apparent brightness.

The tapetum of Placentals was first adequately described by Brücke (1845) and thereafter the subject has received much study ; its histological characteristics were fully elucidated by Sattler (1876) while its ophthalmoscopic variations were beautifully illustrated by Johnson (1901) (Plates XIV and XV). It lies in the upper posterior part of the fundus with a preference for the temporal side which is used for forward vision. Ophthalmoscopically it appears as a bright area in the fundus, usually of triangular shape with its base horizontal just above the optic disc, sometimes lying entirely above this structure (horse), sometimes including it (cat) ; it varies, however, considerably in extent, being unusually large in the Cetaceans (dolphins and whales), while in the Pinnipedes (seals) it occupies the entire posterior area of the fundus up to the equator and beyond on the temporal side. In the tapetal area pigment is lacking in the retinal epithelium to allow the transmission of light, and, lying between the choroidal layer of vessels and the choriocapillaris, it is traversed by small vessels to supply the latter, visible ophthalmoscopically as stellate dark dots on the bright background—the “ stars ” of Winslow. The tapetum does not appear ophthalmoscopically in the puppy until some weeks after birth (Usher, 1924).

Histologically two types of tapetum are found, both completely different in origin and structure—the tapetum fibrosum and the tapetum cellulosum (Figs. 579 and 580).

The TAPETUM FIBROSUM develops from the thin layer of elastic fibres found normally in the inner layer of small vessels of the choroid (Sattler, 1876). It is composed of dense fibrous tissue the fibres of which are closely woven together so that the entire structure glistens like a piece of fresh tendon. Among Placentals such a tapetum is typically found in the Ungulates, among which it is almost universal

¹ The unique structure of the choroid of the larger bats will be noted subsequently, p. 459.

² *Tapetum lucidum*, bright carpet.

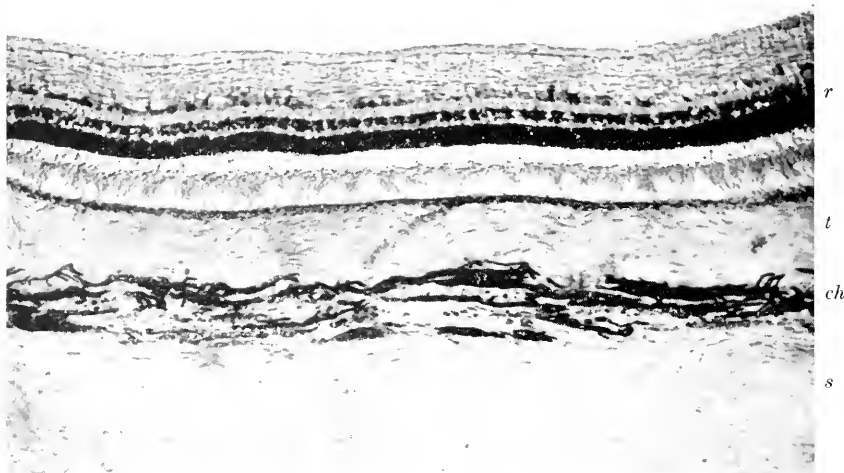


FIG. 579.—THE TAPETUM FIBROSUM OF THE HORSE.

Showing the dense closely-woven layer of fibrous tissue; *ch*, choroid; *r*, retina; *s*, sclera; *t*, tapetum ($\times 126$) (Norman Ashton).

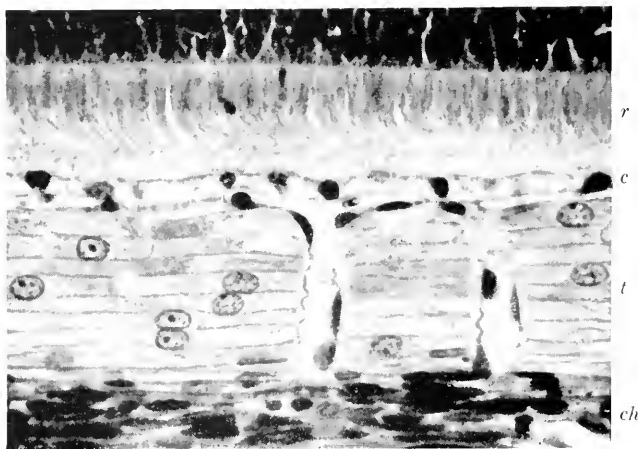


FIG. 580.—THE TAPETUM CELLULOSUM OF THE KITTEN.

Note the beautifully arranged tiers of endothelial cells traversed by small vessels running from the choroid to supply the choriocapillaris. *c*, choriocapillaris; *ch*, choroid; *r*, retina; *t*, tapetum ($\times 375$) (Norman Ashton).



Peccary

(including the elephants) with the exception of the Suoidea (pig, peccary, hippopotamus) and the Tylopoda (camels, llama): it also occurs in the Cetaceans (whales and dolphins), in two Rodents, the spotted eavy, *Cuniculus*, and the flying squirrel, *Pteromys magnificus*, and in the only nocturnal Anthropoid (the night monkey, *Nyctipithecus*, in which it is extremely brilliant).

The TAPETUM CELLULOSUM, on the other hand, develops from the almost continuous layer of endothelial cells which separates the elastic layer from the choriocapillaris (Sattler, 1876). It is formed of several closely set layers¹ of thin, flat endothelial cells arranged in tiers with mason-like regularity resembling plant tissue rather than animal, each cell being packed with rod-like, doubly refracting crystals of an unknown chemical composition (? lipid) (the *iridocytes* of Bruni, 1922) (Mürr. 1925-27). Such a tapetum occurs in all Carnivores (except two Viverrines, *Cynictis* and *Suricata*) including the Pinnipedes, and also in Prosimians—the lemuroids, *Loris*, *Nycticebus*, *Galago* and *Lemur catta*.



Suricate

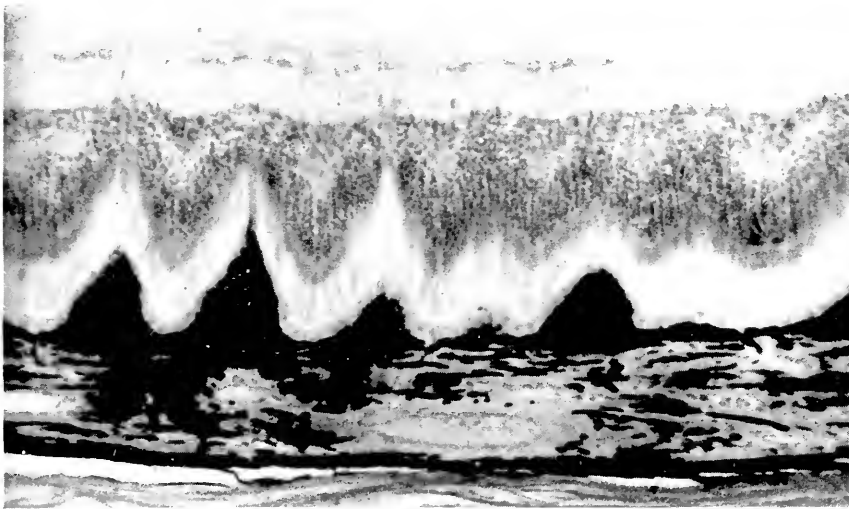


FIG. 581.—THE PAPILLATED CHOROID OF THE FRUIT-BAT (FLYING FOX),
PTEROPUS POLIOCEPHALUS (O'Day).

It is interesting that the pigment epithelium of the retina in Mammals is rarely densely pigmented nor is the pigment migratory. It may contain reflecting material: this in some fruit-bats (*Pteropus*) serves as a RETINAL TAPETUM in the upper part of the fundus, and in the dog is said to augment the effect of the choroidal tapetum.

VASCULAR CHOROIDAL PAPILLE are a unique phenomenon in the animal world found among the Megachiroptera—fruit-bats or flying foxes (*Pteropus*, *Epomophorus*) Kolmer, 1910-24; Fritsch, 1911; Gérard and Rochon-Duvigneaud, 1930) (Fig. 581). These structures which stud the fundus from the ora to the optic disc, form conical mesodermal papillae each with a vascular core, and on this irregular surface the visual cells of the retina are arranged like trees on a range of hills. Although the retina is entirely avascular all its layers are thus



Flying fox

¹ 4 in the wolverine: 8-10 in the lion; 10 in the dog; up to 35 and of a very large size in the seals.

intimately supplied with choroidal capillaries ; to a certain extent, also, the irregular arrangement of the visual cells in the hills and craters may act as an accommodative device.¹

It is interesting that Rohen (1954) found in the dog thick longitudinal muscular layers in the walls of the posterior ciliary arteries and in the arteries of the posterior part of the choroid which he interpreted as a vascular shunt-apparatus regulating the flow of blood into the choroid. Such a mechanism he failed to find in the cat, rabbit, rat or guinea-pig, or in man.

The Ciliary Region. The size and topography of the ciliary region in Placentals vary considerably, the dominating factor being the presence or absence of an accommodative mechanism. Derived from nocturnal ancestors few Placentals, particularly of the lower species, have any marked degree of accommodative activity ; this, indeed, is found

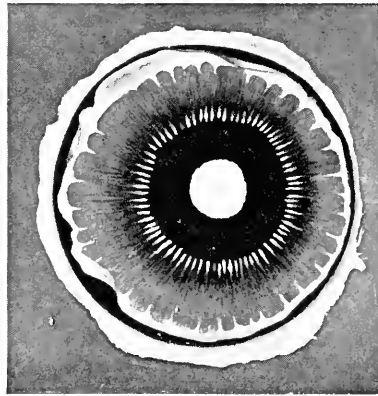


FIG. 582.—THE CILIARY BODY OF PRIMATES.

The inner aspect of the anterior part of the eye showing the ora serrata, the pars plana, ciliary processes and posterior surface of the iris.

only in the squirrels (*Sciuridæ*), the large Carnivores and the Primates. On this essentially depend the size of the ciliary body, its muscular development, the prominence of the ciliary processes, and the configuration of the angle of the anterior chamber. In most small-eyed primitive types with comparatively large lenses (*Insectivores*, *Rodents*, etc.) the ciliary body is small and narrow with miniature processes ; in the shrews it is a simple roll without processes, as in snakes.² In large-eyed Placentals, it assumes the prominent triangular shape with well-developed processes such as are seen in man. It is noteworthy, however, that from the aspect of pure anatomy, in many species a considerable degree of asymmetry exists ; thus in animals with an ovoid cornea (and pupil) the circular ciliary body encroaches far into the iris nasally and temporally, rendering the horizontal segment of

¹ p. 643.

² p. 386.

the pupil relatively immobile, while in many species (Ungulates and Carnivores) the tendency towards nasal asymmetry of the globe in the interests of binocular vision results in a curtailment of the ciliary region and the practical disappearance of the orbicular zone on the nasal side (Fig. 582).

The main determinant in the configuration of this region is the degree of development of the ciliary muscle¹ (Figs. 583–90). Anteriorly the ciliary body splits into two leaves; one, the outer or scleral part, essentially muscular in structure, hugs the sclera as it runs to the corneo-scleral junction; the other, sometimes fibrous, sometimes muscular,

FIGS. 583 TO 586.—THE CILIARY REGION IN MAMMALS.

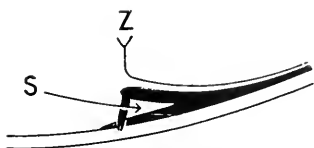


FIG. 583.—Rabbit.

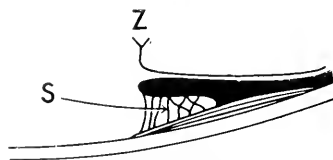


FIG. 584.—Pig.

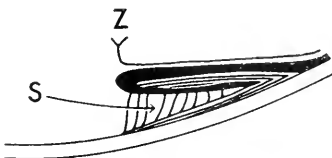


FIG. 585.—Dog.

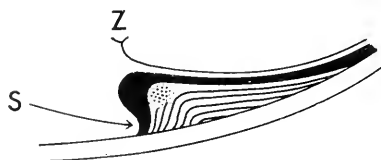


FIG. 586.—Ape.

S, the ciliary cleft (or sinus); Z, zonular ligament. The ciliary muscle where present is indicated by linear shading.

forming the base-plate of the ciliary body, runs inwards towards the root of the iris (Lauber, 1901); between these two leaves lies a triangular cleft of varying depth, the CILIARY CLEFT,² an extension of the anterior chamber which runs backwards deeply into the ciliary region. In the small-eyed and more primitive Placentals (Rodents, etc.) the ciliary muscle is either lacking or very rudimentary and probably functionless; when present it consists of a few slender fasciculi lying in much connective tissue in the outer leaf of the ciliary body (Lauber, 1901; Collins, 1921; Davis, 1929) (Figs. 583, 587). In these animals the ciliary cleft is small. In Ungulates the muscle is also confined to meridional fibres running close to the sclera, prolonged to find attachment to the inner layers of the cornea by the corneo-scleral trabeculae (the cribriform ligament of Henderson, 1921); the inner leaf of the

¹ For the innervation, see Pines and Pinsky (1932), Boeke (1933), Warwick (1952).

² This formation is often known as the *ciliary sinus*; I am using the term *ciliary cleft* to distinguish it from the *ciliary venous sinus*.

ciliary body is merely a simple fibrous base-plate of connective tissue (Zimmermann, 1932 ; Bonfanti, 1949) (Figs. 584, 588). In Carnivores the muscle is more fully developed ; both leaves of the ciliary body are provided with meridional muscular fibres, while the inner is provided with radial fibres (Figs. 585, 589). In both of these two classes

FIGS. 587 AND 588.—THE CILIARY BODY OF RODENTS AND UNGULATES
(J. Rohen).

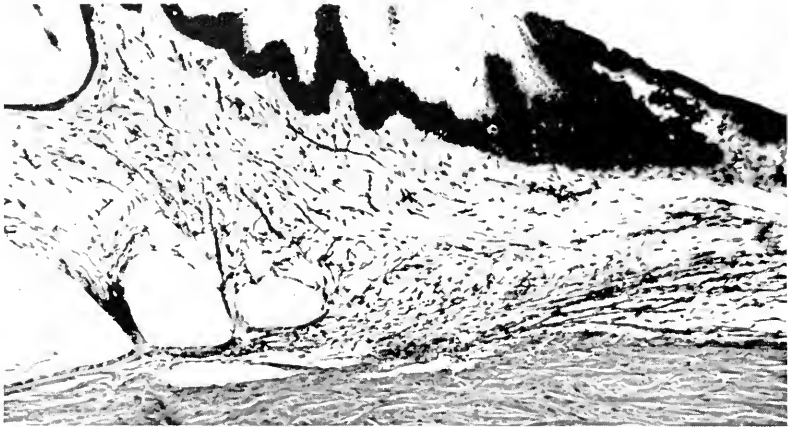


FIG. 587.—Rabbit ($\times 92$).



FIG. 588.—Pig ($\times 21$).

the cleft is wide and deep ; but in Primates the muscle has developed to such an extent that its meridional and oblique fibres occupy the entire ciliary body ; moreover, its massive anterior attachment to the scleral spur (and through it by the scleral trabecule to the deeper layers of the cornea) has almost entirely obliterated the cleft leaving only a remnant of it at the angle of the anterior chamber (Figs. 586,

In the lower Placentals the anterior gap between the two leaves of the ciliary body forming the ciliary cleft deprives the root of the iris of its support and consequently, to serve as anchorage, a series of strands runs from the iris and the base-plate of the ciliary body towards the limbal portion of the cornea where they pierce Descemet's membrane

FIGS. 589 AND 590.—THE CILIARY BODY OF CARNIVORES AND PRIMATES (J. Rohen).



FIG. 589.—Dog ($\times 20$).

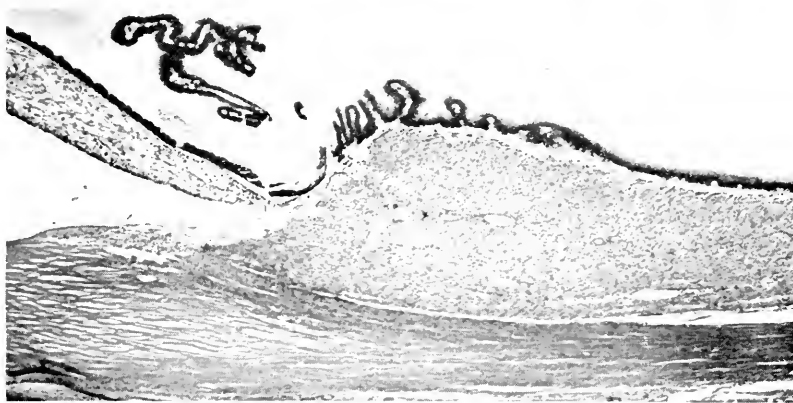


FIG. 590.—Ape ($\times 36$).

and blend with the deeper layers of the substantia propria (Fig. 596). These strands of connective tissue covered with endothelium, bridging over the cleft, constitute the PECTINATE LIGAMENT, which gives support to the root of the iris, the base-plate of the ciliary body and therefore ultimately to the lens. In the lower Placentals wherein the cleft is rudimentary and accommodative strain is lacking and in Primates wherein the cleft is replaced by solid tissue, the pectinate ligament is

rudimentary or vestigial. In Rodents this ligament is made up of innumerable short fibres at the opening of the cleft, which itself is empty (Figs. 583, 591, 596) ; in Ungulates (such as the horse, ox, pig and sheep) the strands over the opening of the cleft are stout and well developed, like the girders of a bridge spanning the ciliary cleft, while the body of the cleft is filled by a close irregular meshwork of fine fibres appearing as spongy tissue (Figs. 584, 592) ; in Carnivora (such as the dog and cat) the more anterior strands supporting the root of the iris are thin and delicate like the cables of a suspension bridge, while the depth of the cleft is filled with fine threads running a fan-like course with no resemblance to spongy tissue (Figs. 585, 593, 597) ;

FIGS. 591 TO 594.—THE ANGLE OF THE ANTERIOR CHAMBER OF PLACENTALS.
As seen gonioscopically, showing the configuration of the pectinate ligament
(from drawings from Troncoso).

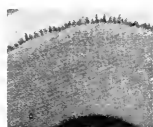


FIG. 591.—Rabbit.

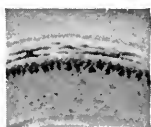


FIG. 592.—Pig.

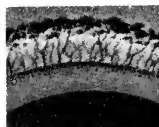


FIG. 593.—Dog.

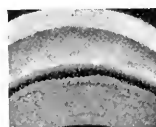


FIG. 594.—Ape.

in the Pinnipedes (seals) the anterior strands are particularly stout. In the Primates (man) the pectinate ligament is discernible until the 6th month of foetal life (Collins, 1899 ; Seefelder, 1910), but owing to its subsequent atrophy it can hardly be said to exist in the adult, the support of the lens being more adequately undertaken by the dense muscular and trabecular tissue of the ciliary body (Figs. 586, 594).

This interesting and important region has received a considerable amount of attention. The first to give an adequate description with illustrations was Murray (1780) at Uppsala who called the cleft at the angle of the anterior chamber of the ox the *ciliary canal*. In the following year, Felix Fontana (1781), the anatomist of Pisa and Florence, gave a description of the same region and since then the extensions of the anterior chamber into the ciliary region of Mammals have variously been called *Fontana's spaces* or *canals*. Shortly thereafter Kieser (1804) of Göttingen pointed out that such structures did not exist in man. Subsequently Hueck (1839) of Dorpat, studying the cow's eye, described the teeth-like structures stretching over Fontana's spaces from the root of the iris to the sclero-corneal junction as the *pectinate ligament* (*pecten*, a comb), an appropriately descriptive term ; since then it has been called by many names—the *suspensory ligament of the iris*, the *iris pillars*, and so on (Fig. 595).

Over the last century and a half much study has been given to the ciliary region of the mammalian eye—most of it histological.¹ More recently a better perspective has been put on the anatomical arrangements by the gonioscopic

¹Blumming (1868), Iwanoff and Rollett (1869), Angelucci (1881), Dostoiewsky (1886), Virchow (1886–1910), Rochon-Duvigneaud (1892–93), Collins (1899), Asayama (1901), Huber (1901), Seefelder and Wolfrum (1906), Henderson (1908–50), Rohen (1953), and de Toledo Piza (1955).

FIGS. 595 TO 597.—THE ANGLE OF THE ANTERIOR CHAMBER OF PLACENTALS.

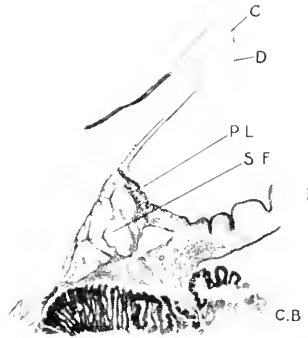


FIG. 595.—DIAGRAM OF THE ANGLE OF THE ANTERIOR CHAMBER OF THE HORSE.

C, cornea; *CB*, ciliary body; *D*, Descemet's membrane; *I*, iris; *PL*, pectinate ligament; *SF*, spaces of Fontana.

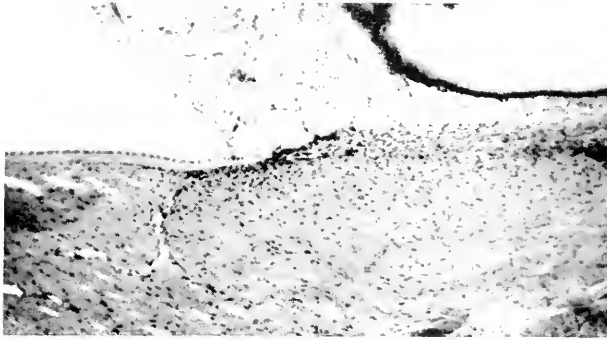


FIG. 596.—SECTION OF THE ANTERIOR CHAMBER OF THE RABBIT.

Note the stout fibre of the pectinate ligament bridging over the entrance of the ciliary cleft and piercing Descemet's membrane ($\times 60$) (Norman Ashton).



FIG. 597. SECTION OF THE ANTERIOR CHAMBER OF THE CAT.

Note the delicate strands of the pectinate ligament filling the ciliary cleft ($\times 60$) (Norman Ashton).

and micro-anatomical methods applied by Troncoso and Castroviejo (1936) and Troncoso (1937). Troncoso called the cleft the *cilio-scleral sinus*, but since it does not separate the ciliary body and the sclera but extends into the ciliary body itself, *ciliary cleft* (or *sinus*) would seem a more appropriate name.

The *ciliary processes* vary considerably in their form, depending on the number and arrangement of the zonular fibres, the development

FIGS. 598 AND 599.—THE CILIARY PROCESSES OF PLACENTALS
(after Franz, 1911).

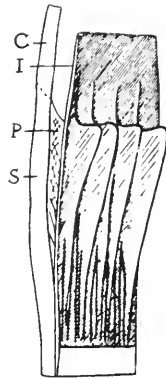


FIG. 598.—*Felis libyca*.

C, cornea; I, iris; P, pectinate ligament; S, sclera.

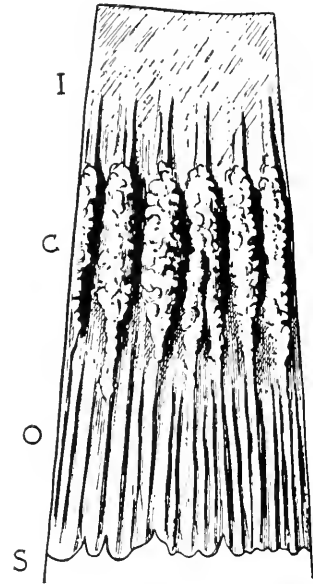


FIG. 599.—*Elephas maximus*.

C, ciliary processes; I, iris; O, orbiculus ciliaris; S, ora serrata.

of which depends on accommodative activity.¹ Three general types exist (Figs. 598 and 599).

1. In the lower orders as exemplified in the Rodents (rabbit), the processes are thin and blade-like with deep valleys between; many of them extend far into the iris as is seen in the human embryo, touching the lens anterior to the equator, so that the corona ciliaris is in large part an iridic structure. The posterior chamber is thus exceedingly small.

2. In the Ungulates as exemplified in sheep, pigs and cattle, the processes are thick and club-like with shallow valleys and are confined

¹ For the comparative anatomy see Würdinger (1886), Bayer (1892), Lauber (1901), Virchow (1910), Franz (1912), Hess (1913), Beauvieux and Dupas (1926), Troncoso (1932), Wislocki (1952), Rohen (1953).

to the ciliary region ; their anterior ends form a solid wall not encroaching upon the iris so that the posterior chamber is deep. The apices of the processes, however, touch the lens.

3. In Carnivora, as exemplified in the cat, dog, and lion, the ciliary processes are of two types—knife-like, tall, major processes between every pair of which lies a small minor process ; none of them reaches the lens. In the Primates the general arrangement is similar but the main ciliary processes are stouter and more rounded and several stumpy minor folds (*plicae ciliares*) lie between the main processes.



FIG. 600.—THE IRIS OF THE FETAL GUINEA-PIG.

Note the *circulus arteriosus iridis major* faintly outlined in the nasal and temporal parts and the vessels of the pupillary membrane spanning the pupil (from a slit-lamp drawing by Ida Mann).

4. Finally, the ciliary processes are absent in the shrews (*Soricidae*).¹

Curious nervous structures have been described in the ciliary body of certain Cetaceans in the region of the angle of the anterior chamber which may perhaps be CILIARY RECEPTOR ORGANS. In the beaked whale, *Hyperoodon*, Pütter (1912) found elongated nervous structures which appeared to be associated with the ciliary nerves, and in the hump-back whale, *Megaptera*, Rochon-Duvigneaud (1943) described oval bodies isolated or lying in groups, resembling pacchionian corpuscles or the corpuscles of Herbst in the bill of the duck. Their function is enigmatic, but it has been suggested that they are sensory pressure-organs of value to the animal when it dives. This may be possible in view of the "corpuscles" described by Kurus (1955) in the ciliary body of man which conceivably may act as receptors to changes in the intra-ocular pressure.

¹ It will be remembered they are also absent in Fishes (except Selachians), *Sphenodon*, lizards and snakes.

The Iris. The deeper layers of the iris conform to the general vertebrate type. Both layers of the retinal epithelium are heavily pigmented except when a dilatator pupillæ muscle is present in which case the anterior layer lacks its pigment except near the pupillary border. The pupillary muscles are non-striated; a sphincter is always present, massed particularly near the pupillary margin, but sometimes (in aquatic Placentals such as the otter, the Pinnipedes and the Cetaceans, and in the pig) extending peripherally throughout the entire width of the iris; the dilatator is absent in the nocturnal representatives of the lower species.

The main (deeper) mesodermal layer of the iris corresponds with that of other Vertebrates, being supplied by a circular artery (the

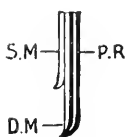


FIG. 601.—STRUCTURE OF THE IRIS OF PLACENTALS.

S.M., *D.M.*, superficial and deep mesodermal layers. *P.R.*, the two posterior retinal layers containing between them the potential cavity of the optic vesicle.

as in the guinea-pig (Fig. 600); from it radial vessels are given off to supply the sphincteric and subsphincteric plexuses, the blood being drained away by a radial system of veins. Superficially to this, however, lies a layer unique to Mammals—the *anterior mesodermal layer*. In embryonic life this layer grows in from the periphery in advance of the deeper layer of mesoderm and the retinal epithelium, carrying with it a rich vascular supply to constitute the anterior portion of the tunica vasculosa lentis. The central (pupillary) portion of this layer is diaphanous and almost acellular and as development proceeds it gradually atrophies, receding to a sinuous scalloped line peripheral to the pupillary margin where the superficial radial vessels anastomose to form a very imperfect circular arcade, the *circulus arteriosus iridis minor*. The site of the lesser circle which marks the limits of the superficial mesodermal layer is fortuitous, sometimes being close to the pupil, sometimes far away; it varies in different species, between individuals of the same species, and in different parts of the iris in the same individual, but the general plan of vascularization remains the same (Mann, 1931) (Fig. 601). In most Placentals this layer is compact and covered by a continuous layer of endothelium; in some Rodents (rabbit) and the higher Primates (*Macacus*, the gorilla and man) it tends to atrophy so that an incomplete layer is formed with the development of open crypts (Wolfrum, 1926; Vrabec, 1952). As we have seen, from its periphery are given off strands of endothelial-lined connective tissue which traverse the angle of the anterior chamber

to find anchorage in the limbal region of the sclera (the pectinate ligament); these are of varying development in different species and are only vestigial in man.

The *pigmentation of the iris* is much more drab and uniform than in many other classes of Vertebrates. Except in albinotic individuals it is derived merely from melanin-containing chromatophores, and depending on their number and the density of pigment within them, the iris is a varying shade of brown, tending to yellow when the pigment is scarce and blue (as often in man) for reasons of optical transmission when the stromal pigment is sufficiently sparse. As a rule the pigment is plentiful and the eye dark brown or almost black, and since the chromatophores lie superficial to and between the vessels, the latter are usually completely obscured; only in albino types can the vascular pattern be made

FIGS. 602 TO 606.—PUPILLARY APPENDAGES IN PLACENTALS.



FIG. 602.—The horse.



FIG. 603.—The gazelle.



FIG. 604.—The goat.



FIG. 605.—The camel.



FIG. 606.—The hyrax.

out. Occasionally and very rarely this simple pigmentary scheme is complicated by the presence of other pigments and iridocytes, a circumstance which gives rise to the green lustre of the eyes of some Carnivores, such as the cat, and some Prosimians. In animals provided with a choroidal tapetum, representative elements of this structure are found in the iris—fibrous elements in Herbivora, cellular in Carnivora (Wolfrum, 1926).

The pupillary margin is occasionally marked by special appendages the purpose of which is presumably to diminish glare. These may be of two types.¹ The first, the *CORPORA NIGRA* (grape-seed bodies or *FLOCCULI* of Kieser, 1803), are immobile and are formed by a proliferation of the pigmented epithelium as highly vascularized cystic protrusions of the marginal sinus.² They occur among the higher Ungulates (Figs. 602 to 605). In the Equidae (horse, etc.) they are relatively simple, being confined to the upper edge of the pupil (Fig. 557); in

¹ For literature, see Bayer and Fröhner (1900), Johnson (1901), Lange (1901), Stein (1902), Zietzschmann (1905), Richter (1909-11), Schneider (1930), Rohen (1951-52).

² The embryonic persistence of the primary optic vesicle between the two layers of epithelium at the pupillary margin.

some Ruminants they are more fully developed, as in the gazelle where they are found both on the upper and lower margins of the pupil, or in the sheep where there are as many as 20, or in the wild goat, *Capra dorcas*, where the mesodermal portion of the iris, beautifully striped, participates in the projection; in the Tylopoda (camel, llama) they reach their fullest development, forming a series of ridges and hollows on the upper and lower margins of the pupil which interlock on miosis (Zannini, 1932).

The second type of structure, called the UMBRACULUM by Lindsay Johnson (1901), is somewhat reminiscent of the operculum of some rays¹ (Fig. 606). In the coneys (hyraxes) it is a flap-like fibro-cellular structure, protruding from the mesodermal portion of the iris 2 mm. from its free edge. It is provided with a fan-like arrangement of (muscular?) fibres and is remarkably contractile; apparently without regard to the amount of light and perhaps under voluntary control, it can be retracted out of the pupillary aperture, extended so as to touch the lower margin of the pupil and almost totally occlude it, or protruded, flap-like, to touch the posterior surface of the cornea. An expansile operculum is also seen in some Cetaceans.

The *pupil* in most Placentals is round, both in dilatation and contraction. A slit-shape on contraction is achieved, however, in some Carnivora either as a protective or an optical device. The slit- or oval-shape is maintained by the arrangement of the fibres of the sphincter, two bundles of which cross above and below the pupil and are continued out to the periphery of the iris, a scissor-like action which compresses the pupillary aperture laterally (Michel, 1881; Eversbusch, 1885; Raselli, 1923; Theiler, 1950; Rickenbacker, 1953) (Figs. 608-10). In the smaller Felidae and Viverridae and in some Hyænidæ and Rodentia, as is well seen in the cat or the chinchilla, the slit-like contracted pupil affords protection to an essentially nocturnal animal against excessive light when basking in the sun. In some of the hyænas (*Hyæna striata*, *H. brunnea*) the contracted slit has a constriction in the middle giving the impression of two pupils (K. M. Schneider, 1930). Among the Pinnipedes, in the seals and sea-lions the pupil is dilated and circular under water, but contracts to a vertical slit in the air (except in the bearded seal, *Phoca barbata*, wherein the slit is horizontal); this is almost certainly an adaptation for aerial vision which will be discussed at a later stage (Johnson, 1901).² The walrus, on the other hand, which feeds on land, has a broad, horizontally oval pupil (Franz, 1934).

While round pupils are the rule among Placentals, oval pupils are found among a considerable number of species—usually horizontally oval among Herbivora and vertically oval among Carnivora, a circumstance

¹ p. 287.

² p. 641.

FIGS. 607 TO 610.—THE PUPILS OF PLACENTALS.



FIG. 607.—THE EYE OF A PONY.

Showing the typically horizontally oval pupil of an Ungulate
(photograph by Michael Soley).

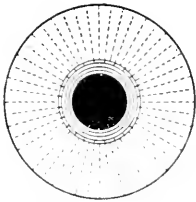


FIG. 608.—Primate.

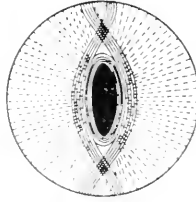


FIG. 609.—Cat.

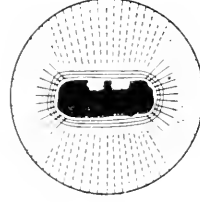


FIG. 610.—Horse.

The round pupil is characteristic of diurnal and strictly nocturnal types. The vertically oval pupil is characteristic of nocturnal types which bask in the sun. The horizontally oval pupil is characteristic of Ungulates and several other types (see text).

In the round pupil the sphincter muscle (solid lines) and the dilatator muscle (broken lines) are symmetrically arranged. In the vertically oval pupil part of the sphincter muscle surrounds the pupil but criss-crossing fibres extend above and below to the periphery of the iris. In the horizontally oval pupil most of the sphincter fibres encircle the pupillary aperture but other fibres are orientated radially on each side to be anchored in connective tissue (shown stippled in Fig. 610) in the nasal and temporal parts of the iris; these areas are devoid of dilatator fibres (from drawings by Eversbusch and Gordon Walls).

depending not on diet but on habit, an adaptation in the first case to suit diurnal, shade-loving animals, in the second, crepuscular or nocturnal animals requiring protection from glare during daylight (Figs. 607–10).

The following have vertically oval pupils :

Many Carnivora—the larger Felidæ (lion, tiger, leopard, jaguar) ; Canidæ (dog, fox, etc.) ; most hyænas, and Viverridæ ; among the Procyonidæ, the panda ; some Ursidæ (the arctic white bear, *Thalassarcos maritimus*, and *Melursus* (Fig. 609)).

Few Rodents—the varying hare (*Lepus timidus*), the nutria-bearing coypu



Vizcacha



Mongoose



Weasel



Coati



Aard-vark

(*Myocastor coypus*), the S. American vizcacha (*Lagostomus trichodactylus*), the Patagonian cavy (*Dolichotis patagonica*), the chinchilla, and the American capybara (*Hydrochærus capybara*).

Few Prosimians—*Nycticebus* and the galago of Zanzibar (*Galago zanzibaricus*).

The following Placentals have horizontally oval pupils :

Among the Ungulates, all Artiodactyls (Suoidea, Tylopoda and Ruminants), all Perissodactyls (Equidae, Rhinocerotidae) except the Tapiridae (Figs. 607, 610).

All Cetaceans (whales) and Sirenians (sea-cows) except *Manatus inunguis*.

Among the Carnivora—a few Viverridae (the mongoose, *Herpestes* ; *Cynictis* and *Suricata*) ; a number of Mustelidae (the ferret, *Putorius furo*, the weasel, *Mustela nivalis*, the ermine, *M. erminea*, the mink, *Lutreola*, the wolverine, *Gulo*) ; among the Procyonidae, the coati (*Nasua*). Among the Pinnipedes, the bearded seal (*Phoca barbata*).

Among the Rodents, the common squirrel (*Sciurus vulgaris*), the African squirrel (*Xerus*), the American chipmunk (*Tamias*), the prairie-dog (*Cynomys*), the marmot (*Marmota*).

Among the Tubulidentata, the aard-vark (*Orycteropus*).

The direct *pupillary reaction* to light is generally present (Hertel, 1907 ; K. M. Schneider, 1930 ; Kahmann, 1930-32 ; Rochon-Duvigneaud, 1933 ; Studnitz, 1934 ; Nordmann, 1947) ; a consensual reaction has been noted in many species (cat, dog, ox, horse, sheep, etc.) (Steinach, 1890-92 ; Schleich, 1922). Dilatation to stimuli such as pain or attention occurs in such species as the cat, the dog and monkeys (*Macacus*) (Levinsohn, 1902 ; Amsler, 1924 ; ten Cate, 1934). reactions particularly evident in the hyæna (Schneider, 1930). The pupils of Ungulates are remarkably insensitive to all stimuli in comparison with those of other Mammals, but the pupils of all Placentals react to atropine (Johnson, 1901).

*The channels draining the aqueous humour from the angle of the anterior chamber are relatively simple in most Placentals.*¹ Associated with the outer wall of the ciliary cleft there is a rich network of veins and venous capillaries which combine to form an intrascleral plexus, the main part of which lies about the level of the middle of the cleft ; this drains outwards by some 5-6 wide scleral veins to the sub-conjunctival veins (Fig. 611). Originally described by Hovius (1716) in the dog, and often called the CIRCLE OF HOVIUS, this plexus varies considerably in richness and complexity in different animals, being relatively sparse in Ungulates and elaborate in Carnivores. That these vessels are the essential exit-channels of the aqueous humour has been shown by the injection experiments of Nuel and Benoit (1900), Seidel (1923-24) and Kiss (1942-49), and when they reach the subconjunctival plane some of them may contain pure aqueous undiluted with blood (in the rabbit, Schmerl, 1947 ; Weekers and Prijot, 1950 ; Greaves and Perkins, 1951 ; Wegner and Intlekofer, 1952 ; Binder and Binder, 1953). According to Rohen (1956) in the dog this plexus anastomoses

¹For literature, see Lauber (1901), Maggiore (1917), Troncoso and Castroviejo (1937-42).

with branches of the anterior ciliary arteries with shunt-like vessels which can be opened or closed by large epithelioid cells. In the Primates, as we have seen, the ciliary cleft is obliterated by the great development of the ciliary muscle, thus cutting off the possibility of the drainage of aqueous by this route ; to maintain connections with the anterior chamber a special sinus, the CANAL OF SCHLEMM, is thus developed as a diverticulum from the intrascleral venous plexus.

FIGS. 611 AND 612.—THE DRAINAGE CHANNELS FROM THE ANGLE OF THE ANTERIOR CHAMBER IN PLACENTALS.

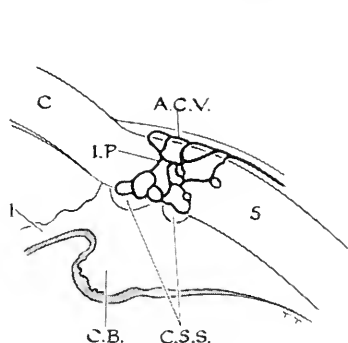


FIG. 611.—A lower Placental (rabbit).

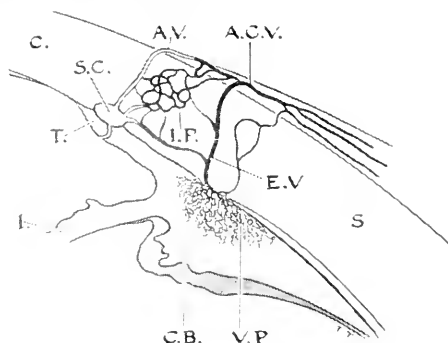


FIG. 612.—A higher Placental (Primate).

A.C.V., anterior ciliary veins ; *A.V.*, aqueous vein ; *C*, cornea ; *C.B.*, ciliary body ; *C.S.S.*, ciliary sinus ; *E.V.*, efferent ciliary veins ; *I*, iris ; *I.P.*, intrascleral ciliary plexus ; *S*, sclera ; *S.C.*, canal of Schlemm ; *T*, trabeculae traversed by a canal of Sondermann ; *V.P.*, ciliary venous plexus.

In Fig. 611 the essential drainage is from the anterior chamber into the ciliary cleft, thence through the intrascleral plexus of veins into the anterior ciliary veins. In Fig. 612 the older channels are represented as in Fig. 611 draining from the ciliary venous plexus, but superimposed on this is a new drainage system represented by Sondermann's canals, the canal of Schlemm, an anterior extension of the intrascleral venous plexus, together with the intrascleral and aqueous veins emptying directly into the anterior ciliary veins.

placed anteriorly at the corneo-scleral junction at which level the angle of the anterior chamber is now closed (Fig. 612). This structure, which may branch to have more than one lumen and is lined by a single layer of endothelium, runs circumferentially around the globe separated from the anterior chamber by the corneo-scleral trabeculae through which pass minute channels, the canals of Sondermann (1933), and is connected to the intrascleral venous plexus by numerous efferent channels, some of which reach the subconjunctival region directly as aqueous veins. This system, added to the intrascleral venous plexus to compensate for the closure of the ciliary cleft, plays the major part in the drainage of the aqueous humour in the eyes of Primates.

The *lens*, suspended freely from the ciliary processes, is usually relatively small and lenticular in shape in diurnal species, the anterior surface being usually the more convex in Carnivora, the posterior in Herbivora and Primates (Figs. 613 to 616); it approaches rotundity and is larger in nocturnal species, especially in the small-eyed lower forms, and is round in aquatic species such as the Cetaceans and Pinnipedes. Among Sirenians (sea-cows such as the manatee and dugong) the lens is lenticular in shape but, to suit the optics of an

FIGS. 613 TO 616.—THE LENSES OF PLACENTALS.

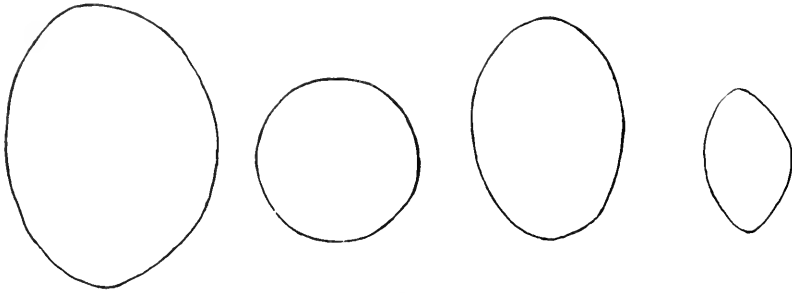


FIG. 613.—Pig.

FIG. 614.—Seal.

FIG. 615.—Dog.

FIG. 616.—Primate.

aquatic environment, approximated closely to the cornea so that the anterior chamber is very shallow. In the tree-shrew, *Tupaia*, and in most squirrels (Sciuridae, except the nocturnal flying squirrels), the lens is tinted yellow (Merker, 1928; Walls, 1931). With regard to its structure, the same general plan of a series of radial lamellæ is apparent throughout the whole vertebrate phylum, with only minor modifications (Rabl, 1899) (Fig. 617). The sutural arrangements are usually simpler than in man, being made up of two lines having a vertical direction anteriorly and a horizontal posteriorly (*e.g.*, rabbit). This



FIG. 617. THE RADIAL LAMELLÆ OF THE LENS OF THE CH. (after Rabl)

forms a transient stage in the development of the lens of Primates but eventually in these the lines branch into a tri-radiate form resembling the letter Y standing in the erect position anteriorly and the inverted position posteriorly (Figs. 618 to 620). In all adult Mammals, the subcapsular epithelium ends at the equator, but in many of the lower species it extends farther back. The *capsule* is always present and in some animals it is very thick, showing definite striations into layers; thus in the horse at the anterior pole it is about 0.5 mm. thick and is made up of 26 layers. The local variations in thickness are not uniform:

FIGS. 618 TO 620.—SUTURAL ARRANGEMENTS OF THE LENS IN PLACENTALS.

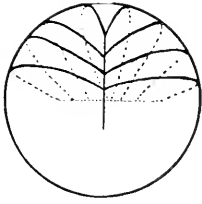


FIG. 618.—The sutural arrangements in a lower Mammal (a rabbit), forming a transient stage in the development of the lens of Primates.

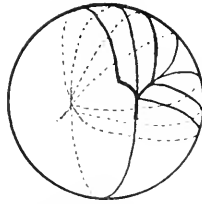


FIG. 619.—The general sutural arrangements in Primates.

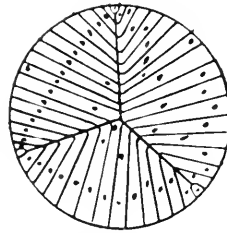


FIG. 620.—The anterior surface of the lens in Primates.

in general, among Sauropsida the maximum thickness is at the equator; in Mammalia the general scheme of the human capsule is followed, but the thinning at the anterior pole which seems to be associated with the formation of an anterior lenticonus during accommodation is peculiar to the Primates (Fincham, 1929) (Figs. 787 to 790).

The differences in configuration in the ciliary body necessitate variations in the arrangement of the *zonular fibres* (Figs. 621–3).¹ In Rodents with ciliary processes prolonged onto the iris the zonular fibres arise from their posterior halves only; in Ungulates they arise from the posterior two-thirds of the processes but hug them anteriorly to their apex. In both cases they run along the floors of each valley and the sides of the adjoining processes to proceed in discrete bands towards the equator of the lens. In Carnivora, however, with their greater

FIGS. 621 TO 623.—THE ZONULAR FIBRES OF PLACENTALS.

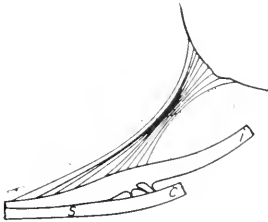


FIG. 621.—An Ungulate (pig).

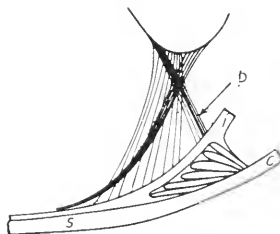


FIG. 622.—A Carnivore (cat).

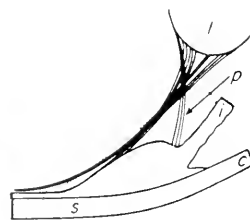


FIG. 623.—A Primate (monkey).

The zonular fibres are outlined in continuous lines, the major ciliary processes in dotted lines. *c*, cornea; *i*, iris; *l*, lens; *s*, sclera. *p* indicates the smaller perpendicular bundles of fibres associated with the minor ciliary processes (from Kahmann and Walls).

¹ For the comparative anatomy of the zonule, see particularly Aeby (1882), Kahmann (1930), Teulières and Beauvieux (1931), Troncoso (1942), Wislocki (1952), Fukamachi (1953).

accommodation, the pattern of the zonule becomes more complex as it traverses the space between the ciliary body and the lens (Fig. 622). Bundles of fibres arise posteriorly from the orbicular portion of the ciliary body, run along the valleys hugging the sides of the major processes and find insertion into the lens anterior to the equator. Other fibres arising more anteriorly pass backwards to find insertion behind the equator, while the space between the two major systems is filled with fibres arising mainly from the minor processes and running perpendicularly to find insertion mainly into the posterior part of the attachment zone of the lens. In the Primates, on the other hand, fibres arising posteriorly in the orbicular region are inserted into the anterior lens capsule, while those arising more anteriorly are inserted into the posterior capsule, the latter being reinforced by perpendicular fibres arising far anteriorly; between these two main systems of fibres a space (the "canal" of Hannover, 1852) exists which is traversed by a few of the fibres of the posterior system finding attachment to the equator itself (Fig. 623).

The *vitreous gel* is constituted as in man, the electron microscope showing a system of fibrils (ox, calf, sheep, pig, rabbit—Schwarz and Schuehardt, 1950; Schwarz, 1951).

FIGS. 624 TO 626.—TYPES OF HYALOID VESSEL (Ida Mann).



FIG. 624.—Fishes.



FIG. 625.—Anurans.

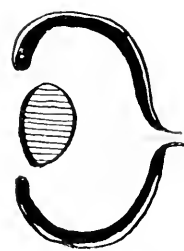


FIG. 626.—Mammals.

FIGS. 627 TO 630.—TYPES OF RETINAL BLOOD SUPPLY IN VERTEBRATES (excluding the falciform process of Teleosts).

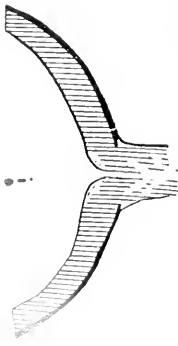


FIG. 627.—The
arteria centralis
retinae.

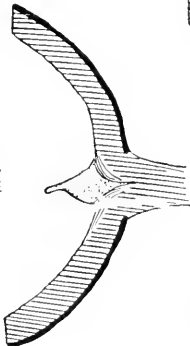


FIG. 628.—The
pecten or conus.

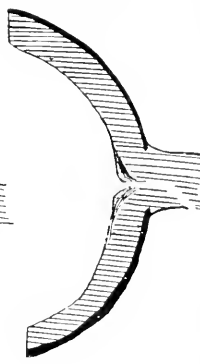


FIG. 629.—The mem-
brana vasculosa
retinae.

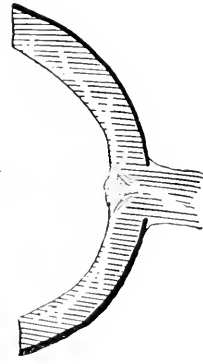


FIG. 630.—The
arteria centralis
retinae.

The Retinal Vascularization

The hyaloid system of vessels is unique in its development in Mammals (Figs. 624–630). We have already seen in Fishes that this system of vessels runs along the ventral part of the globe in the open foetal fissure, an arrangement seen in its most fully developed form in the falciform process of Teleosteans. In many Amphibians this arrangement is extended to constitute a superficial *membrana vasculosa retinae*. In the Sauropsida the hyaloid vessel on entering the eye atrophies except for the formation of a *conus* or *pecten* at the disc itself. In Mammals the hyaloid artery in embryonic life runs directly to the posterior portion of the *tunica vasculosa lentis*, while a multitude of vessels ramifies in the vitreous. These vessels disappear in the later stages of embryonic life, the only visible remnant being a small residuum of glial tissue lying on the optic disc (Bergmeister's papilla). Sometimes this condition remains in the adult mammalian eye so that the retina itself is avascular; more usually vessels grow out from the hyaloid trunk and invade to a greater or less degree the substance of the retina itself; in this event the hyaloid trunk becomes the central retinal artery. With the exception of the eel and a colubrid snake,¹ it is only within the class of Mammals among all Vertebrates that a retina directly supplied by capillaries is found.

The mode of entrance of the central artery varies in different species. It is derived from the ciliary branch of the external ophthalmic, sometimes supplemented by anastomosis with the small internal ophthalmic artery.² In some species such as the rabbit a central artery accompanied by a central vein enters the optic nerve and runs upwards to reach the centre of the disc; there, just before or just after emerging, it divides into nasal and temporal branches (Bruns, 1882; Henderson, 1903; Davis, 1929). In the cat the central retinal artery was found by Davis and Story (1943) to be invariably occluded and vestigial, the retina being supplied by the terminal posterior ciliary branches of the ciliary artery. In the dog, on the other hand, there is no central retinal artery but several posterior ciliary vessels pierce the sclera around the optic nerve-head where they give off retinal branches, appearing at the margin of the disc as *cilio-retinal arteries*. In this animal a central vein is sometimes present but even when it exists it immediately breaks up to leave the eye with the marginal arteries to enter the subarachnoid space (Wolff and Davies, 1931). Subendothelial cushions were described by Moffat (1952) in the ciliary arteries of the dog, the contraction of which might act by shutting off the choroidal blood supply and diverting it to the retina. In the Primates including man, the central retinal branch of the ophthalmic artery supplies the whole retina apart from small anastomoses from the posterior ciliary

¹ p. 390.² p. 498.

arteries through the circle of Zinn (Wybar, 1956), but in the lower Mammals the tendency is for the posterior ciliary arteries to assume greater importance. It is to be remembered, however, that the appearance of arteries emerging from the optic nerve-head onto the retina in a marginal position around the disc, a formation suggestive of

FIGS. 631 TO 634.—TYPES OF PLACENTAL RETINAL VASCULARIZATION
(See also Plates XIV and XV.)

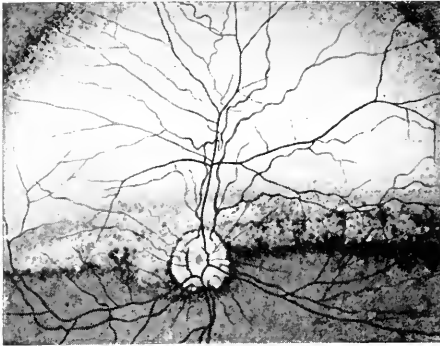


FIG. 631.—THE FUNDUS OF THE DOG.
The lightly coloured area is the tapetum.
There is a venous circle at the disc.



FIG. 632.—THE FUNDUS OF THE CAT.
The lightly coloured area is the tapetum.

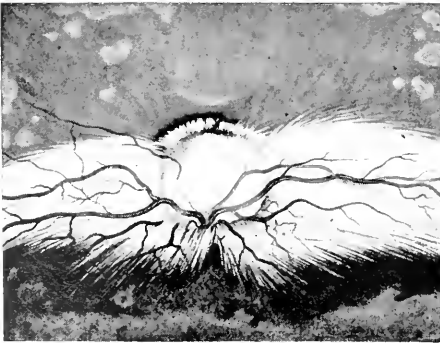


FIG. 633.—THE FUNDUS OF THE RABBIT.
The vessels are confined to the leashes of opaque nerve fibres.

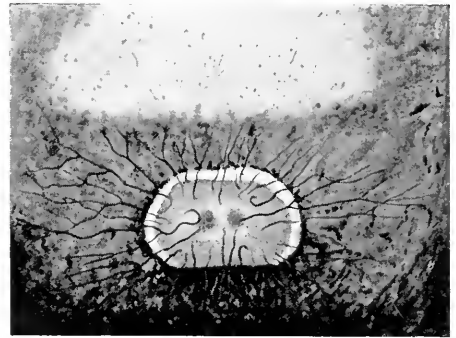


FIG. 634.—THE FUNDUS OF THE HORSE.
The lightly coloured area above the disc is the tapetum.

a ciliary origin, does not preclude their derivation from a central artery that has broken up into retinal branches in the substance of the nerve.

Among the Placentals almost every possible variety of retinal vascularization occurs, ranging from a complete absence of vessels, in which case the retina is nourished entirely from the choriocapillaris, to an elaborate system covering the entire retina in which the capillaries

may penetrate as far as the nuclei of the rods and cones.¹ Leber (1903) divided the retinae of Placentals in this respect into 4 groups :—

(a) **HOLANGIOTIC** (ὅλος, all ; ἄγγειον, vessel) (Plates XIV, XV ; Figs. 631–2). The whole retina receives a direct blood supply either from a central artery or from cilio-retinal arteries which emerge either as a single trunk or as several branches from or around the optic disc. This type of vascularization occurs in some Insectivores (the hedgehog, *Erinaceus*, the mole, *Talpa*), some Rodents (mouse, squirrel, marmot).

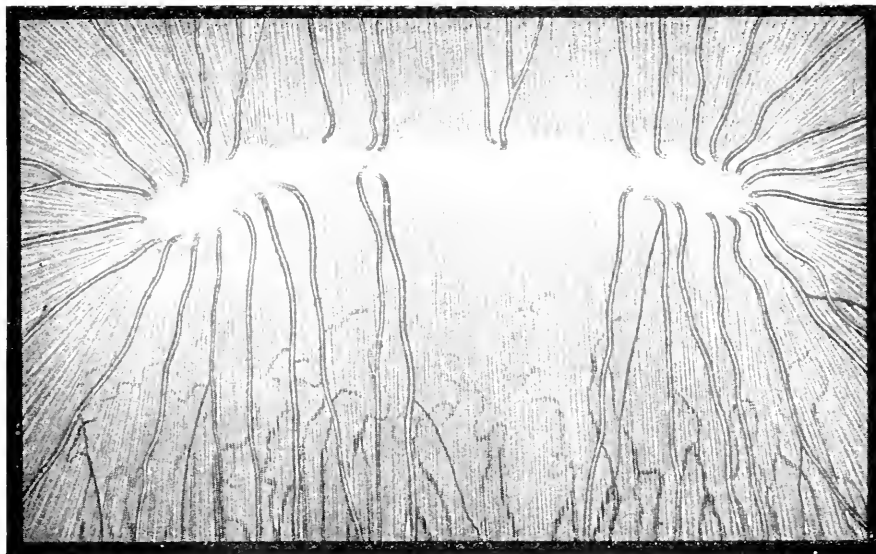


FIG. 635.—THE FUNDUS OF THE SQUIRREL, *SCIURUS VULGARIS* (Lindsay Johnson).

some Carnivores (Felidae, Canidae, Ursidae, some Viverridae and the Pinnipedia), in a few Ungulates (pig, ox), and the Primates.²

In Primates the central artery emerges from the disc as a single vessel, but more usually several large arteries emanate therefrom ; in Carnivores a number of small arteries of the ciliary type emerge from the margin of the disc. In the squirrel and the marmot the disc is a long horizontal line from the entire length of which the vessels emerge (Fig. 635).

(b) **MERANGIOTIC** (μέρος, part) (Fig. 633). Part of the retina is supplied with vessels. This is only seen in the Lagomorpha (rabbit and hare), in which the vessels are limited to the horizontal expansions of medullated nerve fibres (Figs. 633, 637).

¹ For literature, see particularly H. Müller (1861), Sattler (1876), Leuckart (1876), His (1889), Bruns (1882), Barrett (1886), Schultze (1892), Johnson (1901), Leber (1903), Damel and Fortin (1937) (bat), Michaelson (1948–54), Rohen (1954) (rabbit).

² Compare also the Marsupials, *Didelphys* and *Petaurus*, p. 440.

(c) PAURANGIOTIC ($\pi\alpha\rho\acute{\alpha}\nu\gamma\iota\omicron\tau\iota\varsigma$, small) (Plate XV ; Fig. 634). The vessels are very minute and extend only a short distance from the disc. This occurs in Perissodactyla (horse, tapir, rhinoceros which has only capillaries around the disc), the elephant, the Hyracoidea, the Sirenia (*Manatus*, *Halicore*) and among the Rodents in the guinea-pig (*Cavia porcinus*) (Fig. 636).

(d) ANANGIOTIC ($\alpha\acute{\nu}\alpha\gamma\iota\omicron\tau\iota\varsigma$, privative) (Plate XV). The retina is without vessels. This group comprises the more primitive Mammals and includes most of the Chiroptera (bats), the Xenarthra (sloths and armadillos), and certain Rodents (the porcupine, *Hystrix*, the chinchilla, the beaver, *Castor*, and others). Many of these anangiotic

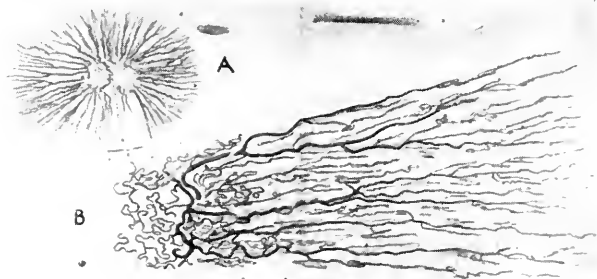


FIG. 636.—RETINAL VESSELS OF THE HORSE.

A, the general arrangement of the retinal vessels. B, a portion of the vascularized retina of the horse showing the peripheral loops, the T-shaped loops between the branches of the main vessel. There are many fine vessels in the optic nerve-head. Specimen injected with Indian ink (after L. Bruns).



FIG. 637.—RETINAL VESSELS OF THE YOUNG RABBIT.

Stained with Indian ink, mounted in glycerine ($\times 16$) (I. C. Michaelson).

PLATES XIV AND XV
THE FUNDI OF PLACENTALS

PLATE XIV
THE FUNDI OF PLACENTALS I

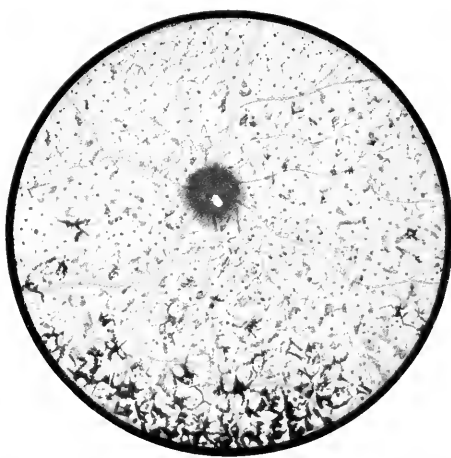
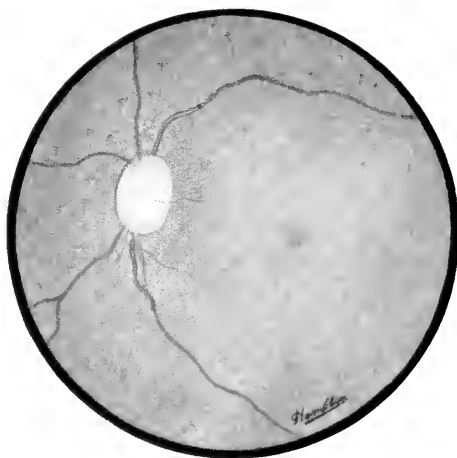


FIG. 1.—The toque monkey, *Macaca pileata*. FIG. 2.—Monteiro's galago, *Galago monteiroi*.

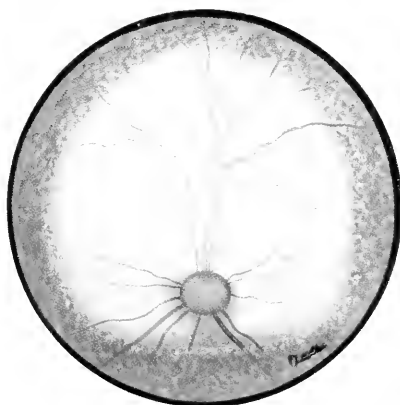


FIG. 3.—The raccoon, *Procyon*.

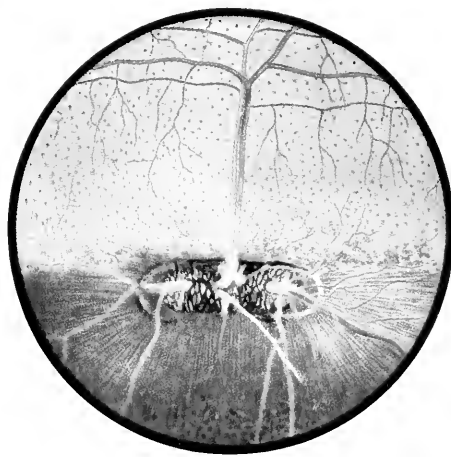
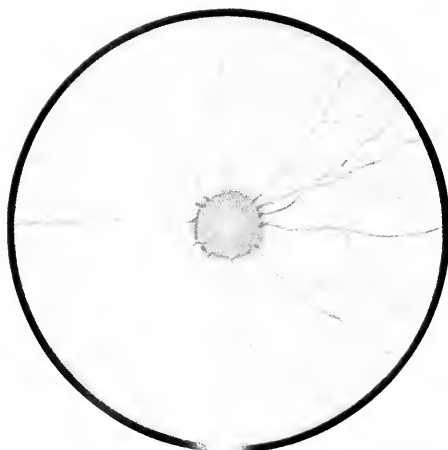


FIG. 4.—The common seal, *Phoca vitulina*.

FIG. 5.—The hog deer, *Cervus porcinus*

(Figs. 1 and 3, Arnold Sorsby; Figs. 2, 4 and 5, Lindsay Johnson.)

PLATE XV
THE FUNDI OF PLACENTALS: II
(Lindsay Johnson)

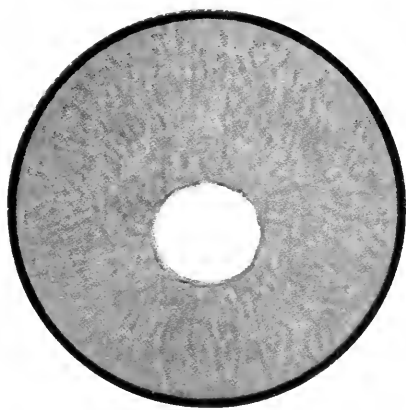


FIG. 1. The Indian rhinoceros, *Rhinoceros unicornis*.

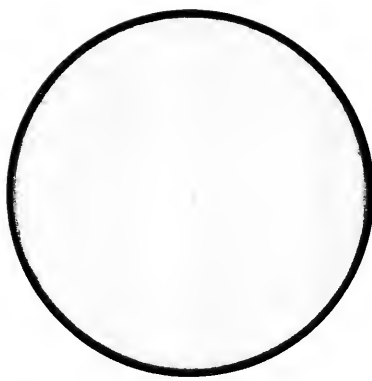


FIG. 2. The Austrabian fruit-bat, *Pteropus poliocephalus*.

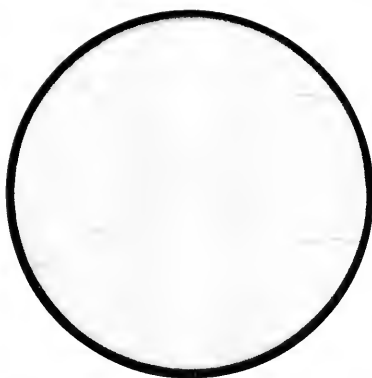


FIG. 3. The common hedgehog, *Ermineus europaeus*.

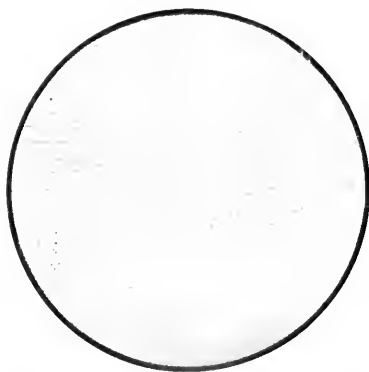


FIG. 4. The flying squirrel, *Pteromys alborufus*.

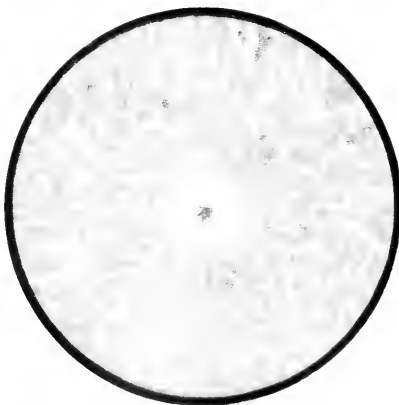


FIG. 5. The Canadian beaver, *Castor canadensis*.

animals, particularly the Rodents, possess a capillary vascularization on the optic nerve-head associated with a button-like projection visible ophthalmoscopically, reminiscent of the papillary conus of Reptiles.¹ A persistent hyaloid artery arising from the disc is more common and is normal in a large number of Rodents and all Ruminants.

The depth to which the vessels penetrate the retina varies considerably. In some Insectivora (the hedgehog and the mole) the large vessels lie superficially, each casting a shadow ophthalmoscopically

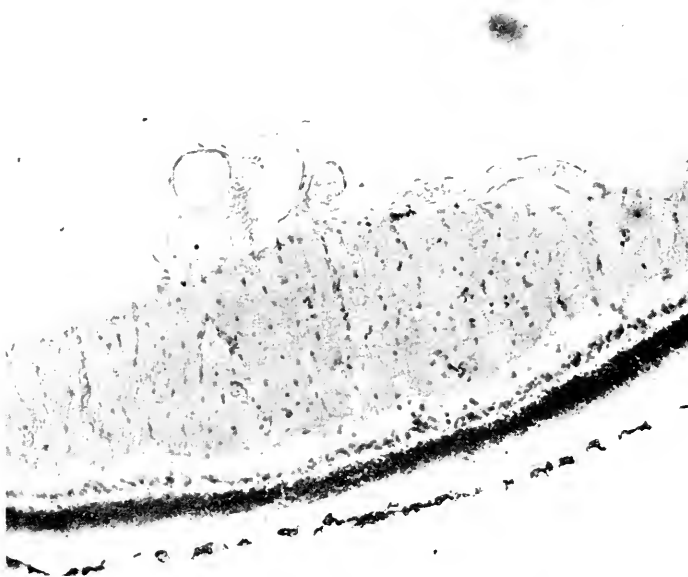


FIG. 638.—SECTION OF THE RETINA OF THE RABBIT.
Including the medullated nerve fibres. The large vessels are clearly pre-retinal (I. C. Michaelson).

(Barrett, 1886) : similarly in some Rodents (mouse, rabbit) they are also very superficial and only partially embedded (Fig. 638). The capillaries may not penetrate so deeply into the retinal tissues as in man. In the horse and the rabbit they reach the nerve-fibre layer only ; in the cat the ganglion layer ; but in most diurnal types with a holangiotic retina the capillaries are reflected in the outer plexiform layer as in man. In these the reticular capillary system is usually well developed and consists of two main networks, an internal lying in the nerve-fibre layer, and an external lying in the outer portion of the inner nuclear layer, the meshes of the deeper net being smaller than the

¹ Compare the Marsupials, p. 440.

superficial. In most cases the superficial net is formed by the end-branches of the arterioles which do not reach the deeper net ; the two nets, however, intercommunicate freely by perpendicular or oblique capillary vessels, while the latter drains into the retinal veins and in all cases there is a zone free from capillaries around the arteries (His, 1880 ; Bruns, 1882). In some species of Rodents, however, members of the family Gliridæ (dormice) such as *Glis* and *Elomys*, and the flying squirrel (*Pteromys*), the capillaries penetrate more deeply, reaching to the outer nuclear layer to supply the bodies of the visual cells and are not reflected until they approach the external limiting membrane (Kolmer, 1929 ; Rochon-Duvigneaud, 1943) ; in these animals it is interesting that the choroid is unusually thin.

It may be useful at this point to summarize the vascularization of the vertebrate retina. The retina is avascular, nourished indirectly from the choroid in Cyclostomes, Selachians, the coelacanth, Chondrosteans, Urodeles, *Sphenodon*, Chelonians, Monotremes, Marsupials (except Macropodidae, *Petaurus* and *Didelphys*), as well as anangiotic Placentals. This source may be supplemented by a specific structure—a falciform process in most Teleosts (except eels, Cyprinoids and goby-fish) and Holosteans ; a conus occurs in lizards and the kiwi (rudimentary in Crocodilians and the Macropodidae) ; a pecten in Birds (except the kiwi).

Direct vascularization occurs by means of a membrana vasculosa retinae in a few Teleosteans (certain eels, Cyprinoids and goby-fishes), Dipnoi, Polypterini, Anurans and Ophidians : in the eel and in *Tarbophis* the vessels penetrate into the retinal substance. Retinal vessels occur only in some Marsupials (*Petaurus* and *Didelphys*) and most Placentals.

The placental retina is of the ordinary vertebrate type with none of the specific peculiarities so frequently evident in other species (Fig. 639).¹ In its general architecture it does not show the same density or purity of lamination as is seen in Birds ; these features are most fully developed in some of the more active diurnal Rodents (the squirrel, *Sciurus* ; the prairie-dog, *Cynomys*). The visual elements in most species are duplex, the rods outnumbering the cones ; the cones are always single and are of simple construction, without oil-droplets or paraboloids (Figs. 266–7). In some of the lowest nocturnal forms rods alone are present (among Insectivores in the hedgehog and the shrew ; in the Chiroptera ; among Xenarthra in the armadillo ; and among Primates in the small nocturnal lemuroids, such as the galago and the loris, and in *Tarsius* and *Nyctipithecus*). The nocturnal Rodents have frequently been said to have a pure-rod retina,

¹ For descriptive anatomy, see H. Müller (1856), Schultze (1866–71), Schiefferdecker (1886), Dogiel (1888), Chievitz (1891), Cajal (1894), Krause (1895), Greeff (1900), Zürn (1902), Detwiler (1924–49), Woollard (1925–27), Uyama (1934) (cat), Kolmer and Lauer (1936) (all classes), Parry (1953) (dog), Vonwiller (1954) (ox), and others. For the structure of the rods of the guinea-pig, see Sjöstrand (1949–53), of the rabbit, see de Robertis (1956), of the synapses of the visual cells see de Robertis and Franchi (1956).

but in the rat, the mouse (Schwarz, 1935), the dormouse (Vilter, 1953) and the guinea-pig (Kolmer and Lauber, 1936 ; O'Day, 1947 ; Vilter, 1949), cones are present although they are very few ; according to Detwiler (1949) they are absent in the chinchilla ; in the Cetacea (dolphins and whales) the cones are also few or non-existent. Only in the Sciuridae (squirrels,¹ and particularly the marmot, the most

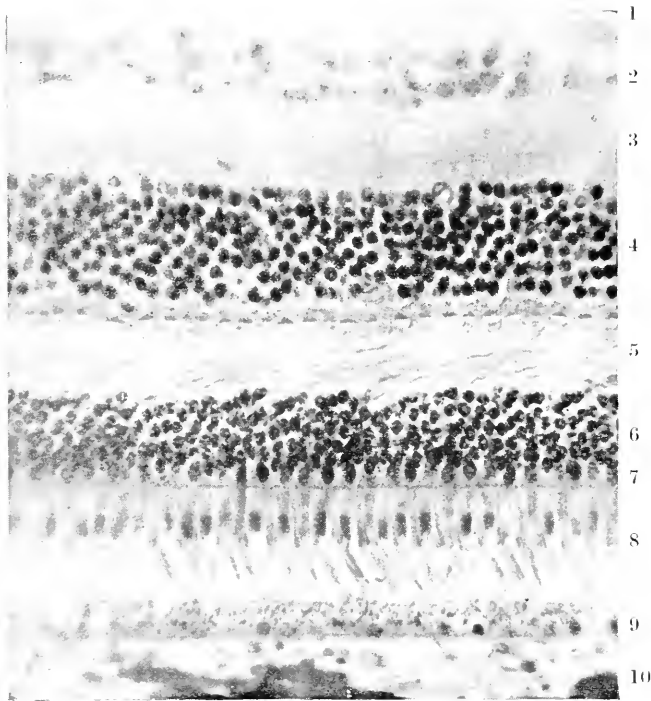


FIG. 639.—A MIXED ROD-AND-CONE PLACENTAL RETINA.

Section through the parafoveal part of the retina of the rhesus monkey (Mallory's triple stain, $\times 480$) (Katharine Tansley).

1, optic nerve fibre layer ; 2, ganglion cell layer ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells ; 9, pigmentary epithelium ; 10, choroid.

diurnal of all Mammals which appears only during daylight) is a pure-cone retina known to exist (Rochon-Duvigneaud, 1929 ; Karli, 1951 ; Vilter, 1954).²

The contrast between the different types of retinal structure in Placentals is best brought out by a comparison between the rod-rich

¹ Except the nocturnal flying squirrel, *Pteromys*.

² For physiological evidence based on the spectral sensitivity, see Arden and Tansley, 1955 ; based on adaptation, see Tansley, 1957.

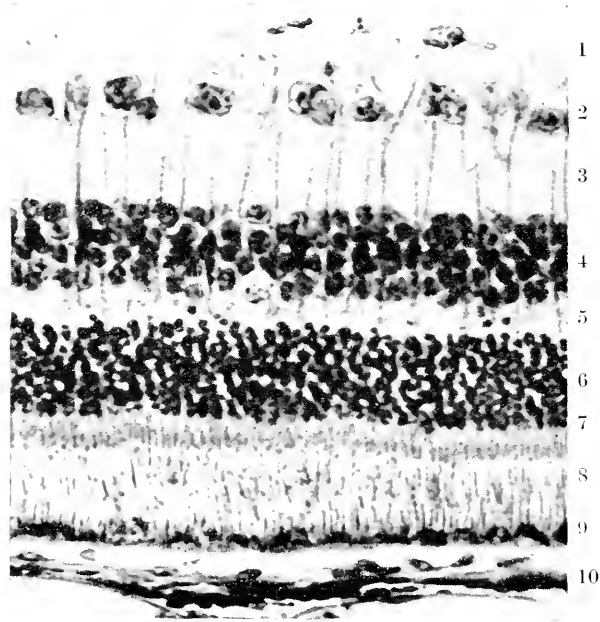


FIG. 640.—THE ROD-RICH PLACENTAL RETINA.
The retina of the rabbit (Katharine Tansley).

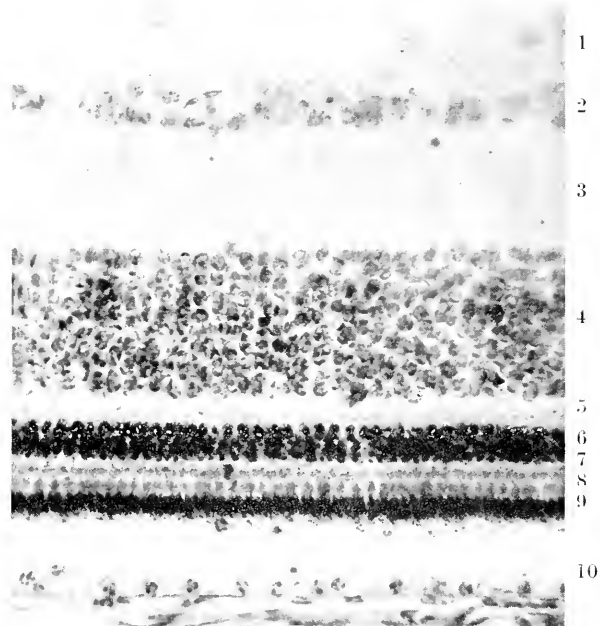


FIG. 641.—THE CONE-RICH PLACENTAL RETINA.
The retina of the squirrel (Katharine Tansley).

1, optic nerve fibre layer ; 2, ganglion cell layer ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells ; 9, pigmentary epithelium ; 10, choroid.

Note the few cells in the ganglion cell layer and outer nuclear layer in Fig. 641 in contrast to the larger numbers in Fig. 640. Compare Figs. 754 and 755. In Fig. 641 note that the cones (8) are in two layers, one behind the other.

retina of the rabbit and the pure-cone (or virtually so) retina of the squirrel (Figs. 640 and 641). In the rod-dominated retina the outer limbs of the rods are long, the outer nuclear layer is thick, there are few ganglion cells and few optic nerve fibres. In the retina of the squirrel, on the other hand, the visual cells themselves are rather unusual and somewhat atypical, being arranged in two layers, one outside the other. Those of the inner layer have long striated outer limbs, while in those of the outer layer this structure is shorter and buried in the pigment epithelium. The inner nuclear layer is unusually thick as also is the ganglion cell layer: there are only 2 to 4 visual cells to each ganglion cell and therefore to each optic nerve fibre, so that the latter layer is again unusually prominent (Arden and Tansley, 1955). According to Vilter (1954) the ratio of cone nuclei to ganglion cells in the souslik, *Citellus*, is 200,000 : 90,000 for the whole retina.

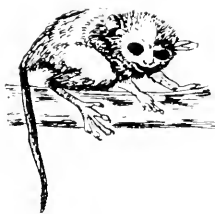
An *area centralis* specifically elaborated for acute vision is found among Placentals, but not commonly (Chievitz, 1891; Slonaker, 1897; Zörn, 1902): most require no specific differentiation for their panoramic vision. When it does occur it may take one of two forms—a band stretching across the posterior part of the fundus or a circular area lying temporal to the optic disc; occasionally both are combined.

A *band-shaped area* is seen in Rodents, most pronounced in the temporal region; in the rabbit it is a broad streak 3–4 mm. wide in its central part running just underneath the optic disc, and throughout its extent the retina is thicker than elsewhere particularly in its rod-and-cone layers and in the layer of ganglion cells (Chievitz, 1891). According to Krause (1895) the content of visual purple is greater within this area than elsewhere; and external to it the choroid is thickened (Davis, 1929). The squirrel has a similar (pure-cone) band but less well defined. Among the Ungulates, some Artiodactyls (Ruminants such as the ox) have a similar band-shaped area running horizontally above the disc and the lower part of the tapetum, associated with a round *area centralis* in the temporal region.

Such a *temporal round area* is common in Ungulates (sheep, goat, horse, etc.); it is also typical of the Carnivores, particularly the Felidae, lying lateral to the optic disc. In this family, particularly in the cat, the tiger and the lion, the *area centralis* becomes highly differentiated; the visual elements (cones, according to Thieulin, 1927) are closely packed and ganglion cells are accumulated in several layers, while there is an external depression (an "external fovea") on the choroidal aspect (Borysiekiewicz, 1887, tiger; Zörn, 1902, cat; Brückner, 1949, lion).¹ In the dog also there are said to be no rods in the central area (Zörn, 1902). Among the Primates a central area is present in the Prosimians (*Lemur catta*, *L. macaco*, etc.) and among the Simians in the nocturnal *Nyctipithecus*. In *Tarsius*, one of the Prosimians, the macular region shows a sudden increase in the number of percipient elements: the number of bipolar and ganglion cells also increases, showing that the elements, although still retaining the morphological characteristics of rods, are assuming the physiological



Squirrel



Tarsier

¹ According to Wöhlflin (1947), who examined a hypnotized lion, the macula is not ophthalmoscopically visible.



Primate
(squirrel monkey)

characteristics of cones. There is, however, no displacement of the bipolar cells or nerve fibres and no true fovea.

A *fovea* occurs only in the Primates, appearing first in *Tarsius*; it and *Nyctipithecus* have a pure-rod fovea (Polyak, 1957). All the Anthropeidea except *Nyctipithecus* have a central area and a well-formed pure-cone fovea of the same type as man, which the retinal vessels approach and encircle but do not invade (Fig. 642) (Woollard, 1926).¹

The *optic disc* in the majority of Placentals is circular as in man, but in some Carnivores (Canidae, as the wolf, jackal, fox) it is kidney-shaped and in many Ungulates and all Equidae it is horizontally oval.



FIG. 642.—THE FOVEA OF A PRIMATE.
Macaca rhesus ($\times 114$) (Katharine Tansley).

In most Sciuridae this is exaggerated to form a unique type—a long, thin, tape-like structure stretching horizontally across the fundus above the axis of vision—which reaches its greatest development in the marmot (Fig. 635); this arrangement gives excellent upward vision for the arboreal family of squirrels. The optic disc lies on the level of the surface of the retina except in Carnivores and the flying squirrel, *Pteromys*, wherein it is sunk to form a deep pit. It varies considerably in colour; usually white or pink, it is red in the Equidae, bright red in the hedgehog and mole, pink surrounded by a green ring in the seal.

The *optic nerve* is of the standard type seen in man, the only exceptional feature being the enormously thick accessory sheath

¹ Blumenbach (1805), Albers (1808), and Soemmerring (1818) in several of the
 2. ...ns; Slonaker (1897) in the gorilla; Wolfrum (1908) in *Macacus*; Franz (1912)
 3. ...lobates; Woollard (1925-27) in several of the Anthropeidea; Detwiler (1943)
 4. ...marmoset and the rhesus monkey.

already noted¹ to be present in whales, the hippopotamus and the elephant; some of the fibres are non-myelinated (Bruesch and Arey, 1942). A minute subdivision of the fibres into fasciculi is common only among Mammals, and there is evidence that the complexity of the glial framework increases in proportion to the visual development of the animal in the evolutionary scale (Deyl, 1895).

The inner architecture and septal system of the optic nerve throughout the Vertebrates is interesting in this respect. As occurs ontogenetically in man, Cyclostomes show merely a central column of ependymal cells which have become invaginated within the developing nerve, and from them processes radiate outwardly towards the periphery. The same arrangement is seen in the Dipnoan, *Protopterus*. In some Selachians and other Dipnoans and in snakes this simple arrangement is reduplicated and the nerve is broken up into a number of bundles each of which has a similar core of cells. In the remainder of the Vertebrates the pattern is altered: oligodendroglial cells (derived from the original ependymal cells) are scattered throughout the nerve. As the visual functions become more highly developed in the higher Vertebrates and man, the fasciculation becomes progressively less obvious, the number of fibre-bundles increasing and the original ependymal system becoming more uniformly dispersed throughout the whole structure.

It is interesting that the *lamina cribrosa* at the optic nerve-head shows wide variations. In general it may be said that in those Mammals which have good day-vision this structure is well developed with many collagenous fibres (squirrel, cat, monkey), while in species with a poor visual capacity (Rodents such as the rat, mouse and rabbit) the lamina is absent and the retina may even herniate in folds into the optic nerve sheath (Tansley, 1956) (Figs. 643-6).

In all Vertebrates below Mammalia the *decussation of the optic nerve fibres* at the chiasma is complete (or practically so in some Reptiles²) so that each eye is connected solely with the opposite side of the brain (Harris, 1904; Kappers, 1921); in all Placentals it is incomplete, but the crossed fibres always remain the more numerous. In Vertebrates below Mammals the fibres remain in distinct and separate fasciculi as they cross: in Placentals they become intimately intertwined and interlaced (Cajal, 1898; Bossalino, 1909). In general the number of uncrossed fibres varies with the degree of frontality of the eyes (Newton, 1704; J. Müller, 1826; Gudden, 1879)³; in animals with laterally directed eyes they are relatively few⁴; they number about 1/6 of the total in the horse,⁵ 1/4 to 1/3 in the dog⁶ and cat,⁷ about 1/3 in the higher Primates, and about 1/2 in Man.⁸ This arrangement whereby corresponding half-fields of each retina are connected to

¹ p. 451.

² Snakes, p. 392.

³ A relationship sometimes referred to as the Law of Newton-Müller-Gudden.

⁴ Rodents such as the rat and rabbit, Bellonci (1884), Singer and Münzer (1888), Pick and Herrenheiser (1895), Brauwer and Zeeman (1925), Overbosch (1926).

⁵ Dexler (1897).

⁶ Vitzou (1888).

⁷ Nicati (1878), Brauwer and Zeeman (1925), Overbosch (1926).

⁸ Brauwer and Zeeman (1925).

THE EYE IN EVOLUTION

FIGS. 643 TO 645.—THE OPTIC NERVE-HEAD OF PLACENTALS.

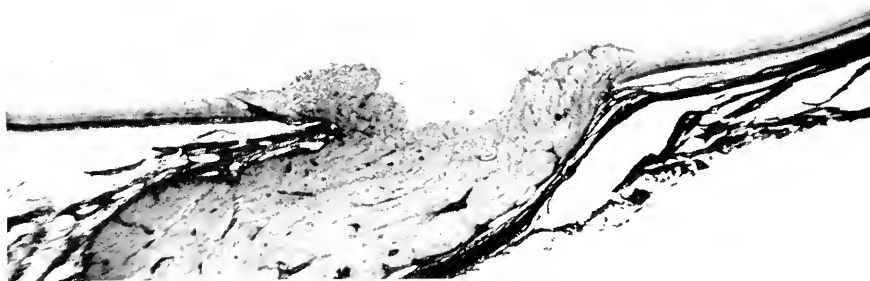


FIG. 643.—THE OPTIC NERVE-HEAD OF THE RABBIT.

Note the absence of collagen fibres at the site of the lamina cribrosa (Kolmer's fixative ; Azan ; $\times 27$) (Katharine Tansley).

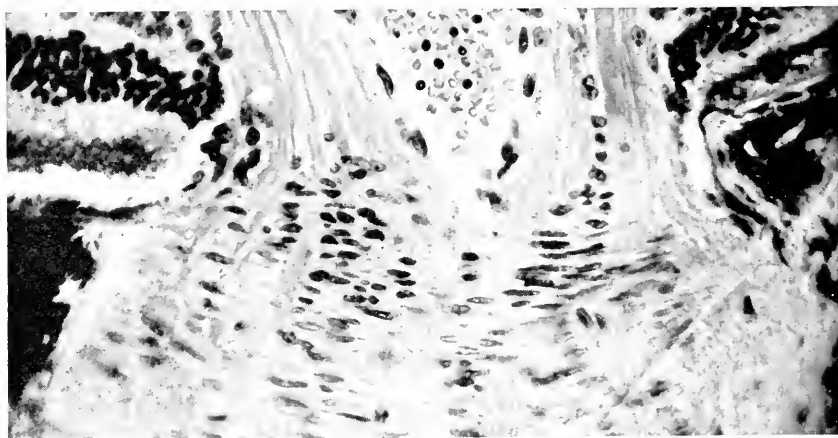


FIG. 644.—THE OPTIC NERVE-HEAD OF THE MOUSE.

Note the band of evenly arranged oval nuclei running across the nerve (Kolmer's fixative ; Feulgen ; $\times 369$) (Katharine Tansley).



FIG. 645.—THE OPTIC NERVE-HEAD OF THE CAT.

Note the well-developed collagenous fibres at the lamina cribrosa (Kolmer's fixative ; Azan ; $\times 50$) (Katharine Tansley).

the same side of the brain lays the foundation for full coordination, visual and motorial, between the two eyes.¹

The semi-decussation of fibres results in great alterations in the finer structure of the lateral geniculate body, the relay station between the optic nerve fibres and the cerebral cortex. It will be seen² that in the lower Vertebrates this structure is insignificant but that in Mammals in which visual projections on a considerable scale are first relayed to the cortex it becomes much more complex, particularly the dorsal nucleus to which this function is assigned. In the lower Mammals this structure is relatively simple and it

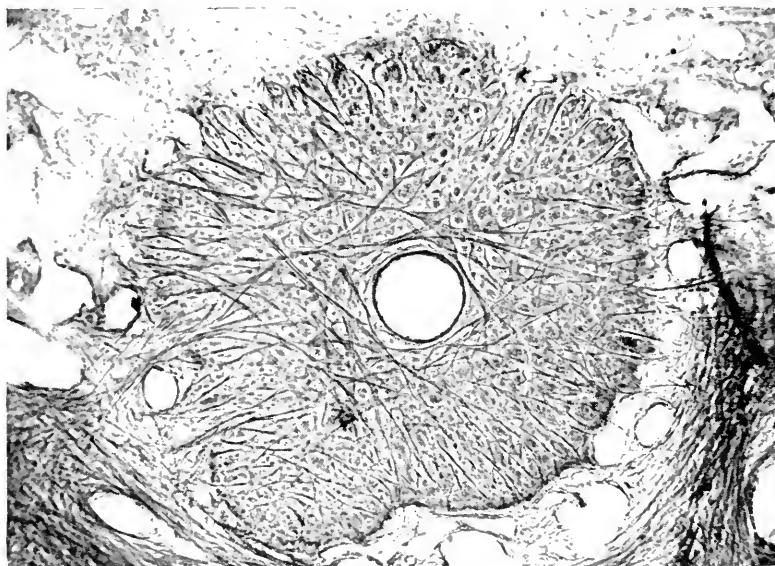


FIG. 646.—THE LAMINA CRIBROSA OF THE KITTEN.

Twenty-four hours before birth (Wilder's stain ; $\times 160$) (Katharine Tansley).

would seem that each optic nerve fibre connects with several cells in the geniculate body which itself shows no ordered lamination. In the Australian opossum, *Trichosurus vulpecula*, an agile arboreal animal, however, the dorsal nucleus shows a four-layered structure (Packer, 1941), while in Carnivores and Primates, six layers appear (Le Gros Clark, 1941-42). This system of lamination is associated with the partial decussation of optic nerve fibres in the chiasma—a characteristic of Mammalia : in the opossum crossed fibres terminate in the 1st and 3rd layers, uncrossed in the 2nd and 4th ; in the Primates crossed fibres terminate in the 1st, 4th and 6th layers, uncrossed in the 2nd, 3rd and 5th layers (Figs. 647 and 648). In the Primates also each retinal cell is projected onto the geniculate body in a point-to-point manner. The reception unit for each of a pair of retinal corresponding points is thus a band of cells involving three laminae, while the projection unit onto the visual cortex is a band of cells involving all six layers.

¹ See further, p. 697.

² p. 541.

THE EYE IN EVOLUTION

FIGS. 647 AND 648.—THE REPRESENTATION OF THE RETINA ON THE EXTERNAL GENICULATE BODY.

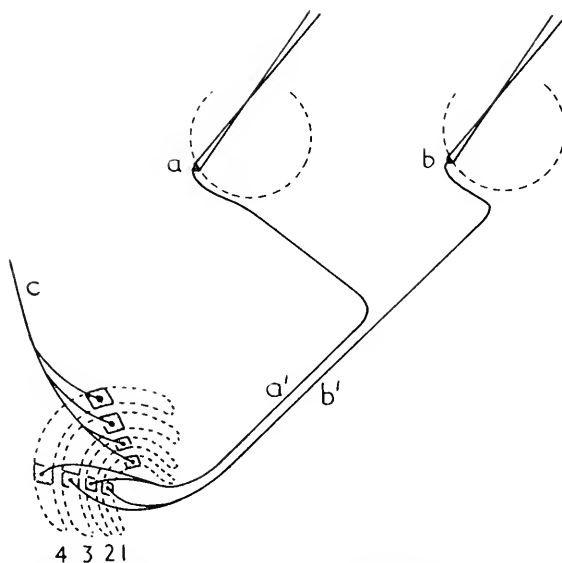


FIG. 647.—IN THE AUSTRALIAN OPOSSUM (after Packer).

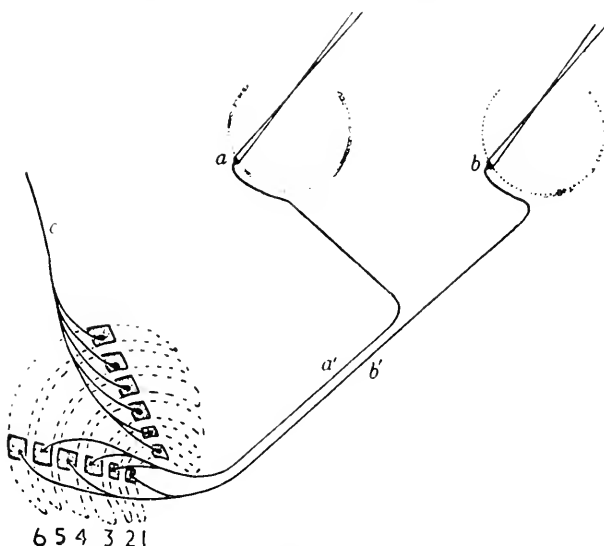


FIG. 648.—IN THE PRIMATE (after Le Gros Clark).

Impulses from corresponding points (*a*, *b*) in the two retinae pass up the optic nerves. Uncrossed impulses (*a'*) terminate in laminae 2 and 4 in the opossum, and 2, 3 and 5 in the Primate. Crossed impulses (*b'*) terminate in laminae 1 and 3 in the opossum and 1, 4 and 6 in the Primate. These fibres terminate in a projection unit in the lateral geniculate body which forms a band of cells running from the hilum of the nucleus. The projection unit from the lateral geniculate body (*c*) to the visual cortex forms a band of cells involving all the laminae in each case.

THE OCULAR ADNEXA

The *conjunctivæ* of many Mammals show large papillæ (horse) or follicles (ox, dog, pig, rabbit) which are not present in the physiological state in man (Bruch, 1853 ; Morano, 1873 ; Miimi, 1935). There is usually an accumulation of pigment, especially near the limbus, but frequently continued into the cornea, contained in branched contractile cells. The transition from the conjunctival to the corneal epithelium is usually gradual, but in some animals (horse) it is abrupt (Zietzschmann, 1904). Variations occur in the conjunctival glands ; thus sweat glands are seen in the bulbar conjunctiva of the pig, the goat and the ox. Small diverticuli filled with epithelial cells somewhat resembling epithelial cell-nests forming tubular depressions near the limbus were first described in the pig as the *glands of Manz* (Manz, 1859 ; Stromeyer, 1859), vestigial traces of which may be seen in man. Their function is uncertain : according to Aurell and Kornerup (1949) they are the remnants of accessory lacrimal glands which develop in the pig in embryonic life, sometimes persisting in the form of epithelial buds and sometimes as tubules with poorly developed lumina.

In the typical Placental, three *eyelids* are present—an upper, a lower, and a nictitating membrane (or third eyelid) ; the aquatic Placentals, however, form an exception.¹ Of the three, the upper lid, as in Selachians, is the more fully developed and with few exceptions (elephant, deer, hippopotamus, mouse) descends more than the lower ascends—a reverse of the action seen in most lower Vertebrates wherein the lower lid is the more mobile.²

It is interesting that Mammalia is the only class wherein spontaneous shutting and opening of the lids or blinking is highly developed ; although sometimes slow, particularly in primitive forms, the blink-movements are usually very rapid, and except in types with completely lateral eyes, the blink reflexes of both eyes respond when one is threatened or touched.

The upper lid always has a stiffening tarsal plate, the lower sometimes ; it is usually comprised of dense fibrous tissue but is occasionally cartilaginous (in the hedgehog, bat and leopard, Anelli, 1936). Embedded in the tarsi and opening on the lid-margin are tarsal (meibomian) glands providing an oily secretion ; in view of the fact that they evolve from the glands of hair-follicles it is understandable that they are found only in Mammals. In Mammals the tarsal glands are usually smaller than in man : they are absent in aquatic types, replaced by Zeis's glands in the elephant, and by sebaceous glands on the caruncle in the camel (Richiardi, 1877). At the external angle they

¹ p. 501.

² The lower lid is the more mobile in Amphibians, Reptiles (except *Anolis alligator* wherein both are equally mobile, and ? Crocodilians) and, with few exceptions, Birds.

are large and modified in some Rodents (Loewenthal, 1931). Glands of Moll are present in many Ungulates (ox, pig), Carnivores (dog, cat), and Primates (apes, man); but in Rodents they are absent (rabbit, guinea-pig, rat, mouse) (Ikeda, 1953). Most Mammals have cilia (Zietzschmann, 1904), the whale, elephant and hippopotamus being exceptions (Matthiessen, 1893); among domestic animals those of the lower lid are rudimentary, while localized absences occur, such as in the mid-region of the upper lid of the horse (F. Smith, 1922). Eyebrows are specialized in many Placentals (particularly the cat) into long tactile vibrissæ; the camel has a somewhat similar formation on its lower lid.

The movements of the two main lids are elaborately controlled by muscles. In terrestrial Placentals they are closed by the contraction of the annular orbicularis oculi muscle with a sphincter-like interlacing system of fibres (Zietzschmann, 1904; Meinertz, 1932-42; Rohen, 1953-54). All are provided with a levator palpebræ superioris, except the aquatic Cetaceans which have a dilatator rimæ palpebrarum distributed round the lids (Stannius, 1846, in dolphins; Virchow, 1910, in whales). The elephant has a depressor palpebræ inferioris similar to the levator of the upper lid (Virchow, 1910), and in Herbivores the external malar muscle serves as a depressor of the former.

The palpebral muscles of Müller are more fully developed in lower Mammals than in man: in aquatic Mammals the fibres are striated, in terrestrial Mammals they are plain. According to Groyer (1903) they are developed in association with the superior and inferior recti: these divide into two parts, one of which is striated and is inserted into the eyeball, the other is inserted into the lids. Owing to the great development of the upper lid, the muscle running to it divides again into two, forming a large levator muscle anteriorly, and a small palpebral muscle posteriorly. In those cases wherein the palpebral muscles are composed of plain fibres, they are supplied by the sympathetic nerve, but where they are striated they are supplied by the nerves to the recti.

The *third eyelid* in Placentals is characteristically rudimentary; although often reinforced by a plate of hyaline cartilage it lacks a specific musculature as is found in so many lower Vertebrates. Entirely passive in its movements, it is rarely functional, slipping over the eye when the globe is retracted. Occasionally, as in the bear and the rhinoceros, it drifts partly across the cornea when the animal becomes sleepy. The mechanism of its movement is much less specialized than in lower Vertebrates, for any muscular elements it contains are merely vestigial. It seems to be forced out from the canthus across the cornea by the propulsive action of the retractor bulbi muscle as it pulls the eyeball inwards; while the return of the membrane, although probably largely due to its own elasticity, may be helped by the opposite action of the orbital muscle of Müller. It is most rudimentary in the

lower forms (Insectivora, Chiroptera, Edentata and Rodentia) and in Primates; in these with few exceptions it is immobile (Law, 1905; Anelli, 1935). In one monkey (*Macacus speciosus*) it is capable of slight movement (Johnson, 1901), and in the aard-vark, *Orycteropus*, it is freely motile over the keratinized cornea, probably acting as an added protection against the formic acid ejected by the ants on which it feeds. In the Carnivora, apart from the Mustelidæ, it is more fully developed, but in the skunk, with its proptosed eyes, it is altogether lacking. In a few Carnivores it is larger (cat, giant panda, bear, deer), while in Ungulates it is most highly differentiated; in these it is sufficiently large to be swept passively but rapidly right across the cornea when the globe is retracted and it is probable that it serves a valuable function in these animals by giving protection to the eyes from long grasses when they graze.

Among Placentals the nictitating membrane has a basis of hyaline cartilage in most domestic animals (horse, donkey, ox, dog, wolf, pig, goat, cat, hare, etc.); in the rabbit (as in Birds) its basis is merely cellular parenchymatous tissue (Naglieri, 1932). Acinous glands resembling the lacrimal gland in structure are also present (Anelli, 1935); muscular fibres are vestigial.

Most Placentals possess two orbital glands. A *lacrimal gland* secreting a watery fluid is situated in the upper temporal quadrant; as is usually the case among Vertebrates it is associated with the more mobile lid, in this class, the upper. We have seen that in terrestrial Amphibians in which the gland first appears in order to maintain the watery environment of their ancestors for the protection of the cornea, it is situated at the medial canthus in association with the lower lid; in Reptiles and Birds it migrates to the outer canthus still maintaining the same association with the lower lid; in Mammals it appears at the lateral angle beneath the upper lid (Lor, 1898) (Fig. 649). The structure of the gland varies: it is tubular in man, but is alveolar in some Mammals (horse, pig, ox; Mobilio, 1912-13); in some animals it empties by a single duct (Rodents). Sirenians,¹ the pronghorn, *Antilocapra americana*, and the mouse family are said to lack a lacrimal gland²; in the pig its secretion is mucoid rather than watery, and in Cetaceans it is oily.³

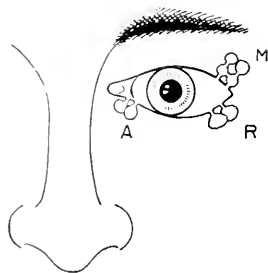


FIG. 649.—THE MIGRATION OF THE LACRIMAL GLAND IN PHYLOGENETIC DEVELOPMENT.

A, position in Amphibians; R, position in Reptiles and Birds; M, position in Mammals (after Wiedersheim).

¹ p. 502.

² A lacrimal gland is also lacking in Cyclostomes, Fishes, aquatic Amphibians, *Sphenodon*, Ophidians, penguins and owls.

³ p. 502.

The tears are drained away by the *lacrimal passages*. Since the lacrimal gland was originally situated at the nasal end of the lower lid, the lacrimal passages are always located in this region. These passages are built on the same general plan throughout the Vertebrates and only minor modifications exist (Walzberg, 1876 ; Lichal, 1915 ; Rochat and Benjamins, 1916 ; Sundwall, 1916). The puncta usually open on the inner surface of the lid, not on the margin as in man. The rabbit has one (inferior) canaliculus (Moncsi, 1906 ; Rochat and Benjamins, 1916 ; Zabojsky-Bruckner, 1924). The sac is rudimentary or lacking in most domestic animals. In some (such as the rat) the nasolacrimal duct is small and inconspicuous. In others (such as the guinea-pig) it is wide with a well-developed ciliated epithelium and surrounded by a rich venous plexus ; in others again (such as the horse) it is relatively narrow (1 to 2 mm.) with several dilatations (1 to 2 cm.) throughout its length (Kelemen, 1950 ; and others). The passages are completely lacking in aquatic types (the Pinnipeds, the Mustelidæ, the hippopotamus, and the Cetaceans) and the elephant (Sardemann, 1884).

The two lacrimal puncta separate a portion of the lower lid to form the caruncle. Since it is isolated from the margin of the lower lid by the development of the canaliculus, the caruncle is absent in those animals which have no lacrimal apparatus (Bromann and Ask, 1910). Frequently its cutaneous origin is emphasized by its continuity with the lid-margin (calf and dog) ; it may be deeply pigmented (Fey, 1914), and contains tubular mucous glands (Caprino, 1955).

Harder's gland (1694), an acino-tubular gland the primary function of which is to lubricate the nictitating membrane, lies on the nasal side of the orbit ; sometimes it is very large extending to a variable extent over the posterior aspect of the globe (particularly in the mouse). According to Miessner (1900) it is absent in the deer, among the lower monkeys it is rudimentary (Giacomini, 1887), and in the Anthropoids and man it is represented only by a transitory foetal structure in the infero-lateral fornix (Loewenthal, 1910).¹ The gland of Harder secretes a sebaceous (Wendt, 1877) or a mucous material (pig, dog, sheep ; Virchow, 1910) which it pours into the conjunctival sac by two ducts.

The *extra-ocular muscles* comprise four recti, two obliques and (usually) a retractor bulbi muscle. The recti are arranged as in man ; the mammalian superior oblique differs from that of lower Vertebrates in the migration of its origin to the apex of the orbit, the reflected tendon being designed to retain the original direction of action (Poole, 1905) (Fig. 188). This mode of development is emphasized in some animals

¹ Harder's gland is also absent in Cyclostomes, Fishes and aquatic Amphibians.

(ass) by the presence of accessory muscles accompanying the reflected tendon ; these represent the direction of the original muscle, while the trochlea is situated at the origin of the primitive muscle from the orbital wall (Zimmerl. 1906 ; Mobilio, 1912). In man similar supernumerary fasciculi have been found as an anomaly, or the more primitive arrangement has persisted (Ledouble, 1897). The insertions of the obliques vary. In man and the chimpanzee the superior oblique is crossed over by the superior rectus, while the inferior crosses the inferior rectus (Fig. 650). In the majority of Mammals both obliques are crossed by the recti (Fig. 651) ; in the tiger the recti pierce the obliques (Fig. 652), and in the lion (as in the tortoise) the superior rectus

FIGS. 650 TO 653.—THE RELATION OF THE OBLIQUE MUSCLES TO THE RECTI.



FIG. 650.—
Man and
chimpanzee.



FIG. 651.—
The majority
of Mammals.

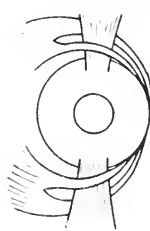


FIG. 652.—
The tiger.



FIG. 653.—
The lion.

pierces the superior oblique, and the inferior oblique pierces the inferior rectus (Fig. 653) (Ottley, 1879 ; Ovio, 1925).

A *retractor bulbi muscle* (*choanoid muscle*, Motais, 1887) occurs in most Mammals; it is particularly developed in Rodents, Ungulates and Sirenians, but is present only in a vestigial form in some monkeys (*Macacus*) and is absent in some of the higher Primates (F. Smith, 1922 ; Bradley, 1933 ; Winckler, 1933 ; Key-Aberg, 1934).¹ The muscle arises from the apex of the orbit, and, running within the muscle-cone, envelops the optic nerve and the posterior part of the globe to be inserted into the sclera behind the recti (Fig. 654). The insertion shows many variations. It may be continuous like the gamopetalous corolla of a flower, or discontinuous with the same general arrangement but in many separate bundles varying in individuals of the same species or even between the two eyes of the same individual, or it may be divided into diverging slips (6 in the sloth-bear, *Melursus labiatus* ; 4 in the cat and dog ; 2 in the whale, etc.) (Fig. 655). It is supplied by nerve VI (Hopkins, 1916), and is usually regarded as a derivative of the lateral rectus (Johnson, 1901 ; Corning,

¹ The muscle is also absent in Cyclostomes, Fishes, Ophidians and Birds.

1900). Its action is probably to pull back the eye, a function eminently required in Herbivora which feed with the head lowered and also in Sirenians which graze at the water's edge ; in man this action is taken over by the tonicity of the recti themselves (Grimsdale, 1921). In the rhinoceros and at least one species of the Ursidæ (*Melursus labiatus*) a simultaneous contraction of the retractor and lateral rectus muscles flicks the eye quickly to the temporal side and at the same time retracts it—a substitute for blinking movements of the lids. A similar movement is seen occurring about once in each minute in the okapi, and as

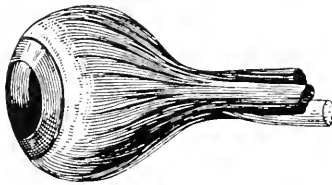


FIG. 654.—THE RETRACTOR BULBI MUSCLE OF A SHEEP (Bland-Sutton).

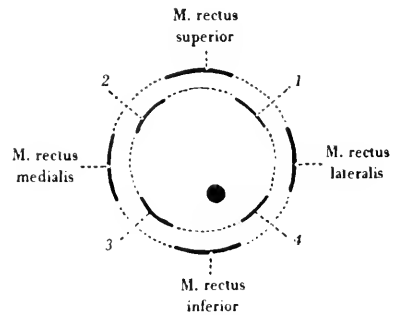


FIG. 655.—THE SCLERAL INSERTION OF THE ORBITAL MUSCLES OF THE DOG.

View from behind. 1-4, the insertions of the 4 heads of the retractor muscle which alternate with and are closer to the posterior pole than the recti (after O. C. Bradley).

the eye retracts the nictitating membrane, well developed as in most Ungulates, sweeps across the globe (Brückner, 1950). As a secondary action it helps to thrust out the nictitating membrane by pressure from behind. Watrous and Olmsted (1941) reported that after excision of all the other extrinsic muscles in the dog, the retractor bulbi was eventually capable of moving the eyeball in all directions.

In the higher Primates the retractor muscle is vestigial or absent. In *Macacus*, the remnant lies above the lateral rectus, and in this region vestigial muscular fibres have been found in man (Nussbaum, 1893 ; Ledouble, 1897 ; Fleischer, 1907). Indeed, according to Lewitsky (1910), there is always a well-marked connective tissue strand in this position in man, running from the back of the fascia bulbi to the apex of the orbit. Whitnall (1911) has reported a case wherein a well-developed muscle of four strands existed (Fig. 656).

The orbital muscle of Müller is found in many Vertebrates (Amphibians, Reptiles, Birds) as a well-developed striated muscle mass ; in Mammals it retrogresses and its fibres become plain. According to

Burkard (1902) it is a derivative of the maxillary musculature, which enters the orbit through the inferior orbital fissure and compensates for the deficiencies of a lateral wall. It is possible that in those animals in which it is well developed it may act as a protrudor muscle by pulling forwards the fascia occupying the fissure and thrusting the eye outwards.

It is curious that despite the elaborate provision of extra-ocular muscles and their comparative size, the ocular movements of most terrestrial Vertebrates are restricted.¹ The eye of the elephant, for example, is almost immobile despite the fact that the size of its extra-ocular muscles is "stupefying" (Soemmerring, 1818), corresponding to the size of the animal rather than to its eye which is relatively small and compares in bulk with that of the ox.²

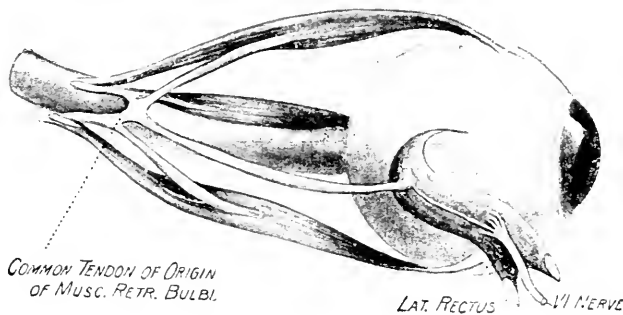


FIG. 656.—AN ABNORMAL RETRACTOR BULBI MUSCLE IN MAN.

Four muscular bundles run forwards towards the globe, each fusing with a rectus before reaching it. One bundle is innervated by nerve VI (indicated in the figure), and the others by nerve III (Whitnall, 1911).

We have seen that among Amphibians the *orbit* opens freely into the cavity of the pharynx; and among most of the lower Vertebrates the postero-lateral wall remains membranous, opening into the temporal fossa, a communication which persists in the higher Mammals and man as the inferior orbital fissure, the anterior end of which (in man) may exceptionally encroach upon the lateral wall to form a "sphenozygomatic fissure" (Tanzi, 1892; Duckworth, 1904). The completeness of the orbital bony walls varies considerably owing to irregularities in the constituent bones: the frontal and sphenoid are always present, the ethmoid and the palatine usually do not participate, and accessory ossicles are common (Maggi, 1898). Among the Rodents the orbit is always open, particularly so in the rabbit; in this animal the floor of the orbit is largely muscular (Davis, 1929). In the elephant and some of the Artiodactyls the orbit is also open and is particularly so among the Carnivores, an adaptation resembling that seen in lizards and snakes

¹ p. 692 *et seq.*

² p. 450.

to allow ample scope for a wide gape of the jaws. On the other hand, among many Ungulates, particularly the horse and all horned animals, the orbit is enclosed and heavily reinforced, as if for protection against the severe injuries caused by horns, and also for strengthening the skull for combat. Among the Prosimians the orbit is incompletely closed, maintaining continuity with the temporal fossa; among the Anthropoidea it is completely enclosed. A lining periorbita is invariably present, associated with muscular elements (Burkard, 1902; Ashley-Montague, 1931). The orbits vary much in position depending on whether the eyes look frontally or laterally (Koschel, 1883)¹; their capacity compared with the size of the globe also varies within wide limits (pig, 2.2 : 1; sheep, 1.6 : 1; horse, 3 : 1; ox, 6 : 1; man, 4.5 : 1, Dexler, 1893). Even among the Primates themselves the size of the orbit varies only very loosely with that of the globe, large Primates having a relatively small orbital capacity (Imai, 1934-36; Schultz, 1940; Chamberlain, 1954).

The vascular system is extremely variable throughout the vertebrate phylum. In man, the entire intra-ocular blood supply and most of the orbital blood supply is derived from the internal carotid artery; in the lower Mammals, the external carotid takes the larger share and sometimes is the sole source of supply. In Rodents such as the rat and the rabbit the arrangements are relatively simple (Fig. 657). The main blood supply to the globe and the orbit is derived from the internal maxillary branch of the external carotid. The external ophthalmic divides into several branches which supply the muscles and tissues of the orbit, as well as the long and short ciliaries which enter the globe. A second artery of supply, the internal ophthalmic artery, is small. It is derived from the circle of Willis and ultimately from the internal carotid; it runs through the optic foramen into the orbit, sends an anastomotic branch to the nasal long ciliary artery and enters the optic nerve near the globe to supply the retina as a central retinal artery (Krause, 1868; Henderson, 1903; Davis, 1929; Daniel *et al.*, 1953; Janes and Bounds, 1955).

Among the Carnivores, the dog and cat may be taken as typical. In the dog the arrangement is not very different from that in the rabbit (Fig. 658). Again, the main blood supply to the orbit and globe is by way of the external ophthalmic branch of the internal maxillary artery which is ultimately derived from the external carotid. In the same way an internal ophthalmic artery derived from the circle of Willis (that is, ultimately from the internal carotid) also enters the orbit to anastomose with the ciliary branch of the external ophthalmic. There is, however, a large anastomotic branch (the *arteria anastomotica*) between the internal carotid and the external ophthalmic arteries, so

¹ p. 672.

FIGS. 657 TO 662.—THE CAROTID CIRCULATION IN MAMMALS
(after Daniel *et al.*, 1953).

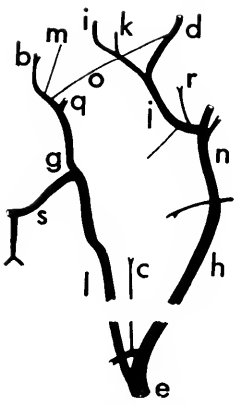


FIG. 657.—The rabbit.

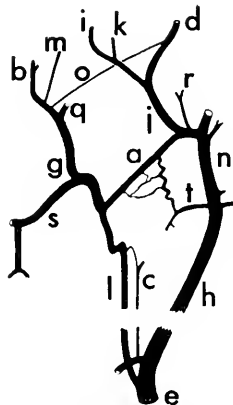


FIG. 658.—The dog.

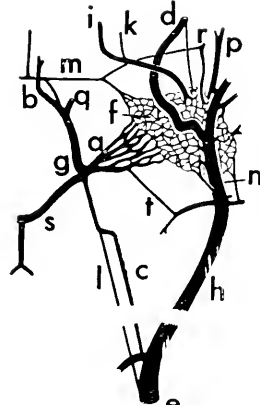


FIG. 659.—The cat.

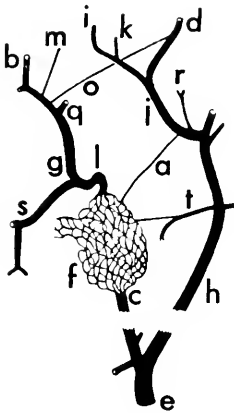


FIG. 660.—The pig.

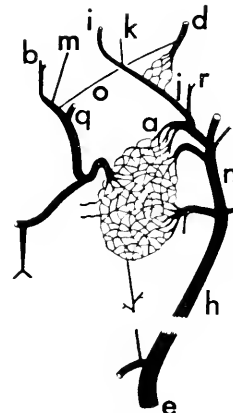


FIG. 661.—The sheep.

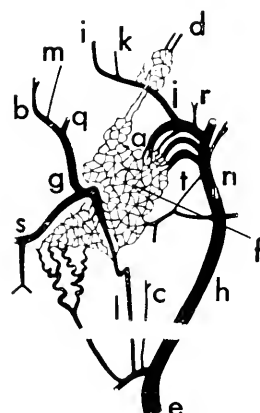


FIG. 662.—The ox.

a, arteria anastomotica ; *b*, anterior cerebral artery ; *c*, ascending pharyngeal artery ; *d*, ciliary artery ; *e*, common carotid artery ; *f*, carotid rete ; *g*, circle of Willis ; *h*, external carotid artery ; *i*, external ethmoidal artery ; *j*, external ophthalmic artery ; *k*, frontal artery ; *l*, internal carotid artery ; *m*, internal ethmoidal artery ; *n*, internal maxillary artery ; *o*, internal ophthalmic artery ; *p*, lacrimal artery ; *q*, middle cerebral artery ; *r*, arteries of extrinsic ocular muscles ; *s*, posterior communicating artery and proximal part of posterior cerebral artery ; *t*, ramus anastomoticus.

large that the intra-ocular circulation can be maintained unimpaired either by the external or internal ophthalmic arteries (Ellenberger and Baum, 1891 ; Henderson, 1903 ; Parsons, 1903 ; Jewell, 1952 ; Daniel *et al.*, 1953). It is interesting that in association with this anastomotic vessel there is a relatively simple arterial network (the

rete of Hürlimann, 1912) situated intracranially in the cavernous sinus.

In the cat the circulation is unique in that the internal carotid in the adult is vestigial, being reduced to imperforate connective tissue strands (Fig. 659). The external carotid, on the other hand, is well developed and its large internal maxillary branch provides the basis of an elaborate anastomotic network (the carotid rete) which is situated extracranially near the apex of the orbit. From this rete large anastomotic vessels supply the circle of Willis by way of the orbital fissure. Also from this rete seven independent trunks (corresponding to the ophthalmic circulation of human anatomy) supply the orbital tissues and the globe. The largest branch of the internal maxillary—the ciliary artery—reaches the optic nerve where it breaks up into its numerous terminal ciliary branches which enter the eyeball; there is no central artery of the retina (Tandler, 1899–1906; Hürlimann, 1912; Daniel *et al.*, 1953; etc.). Davis and Story (1943) found that from the circle of Willis a tenuous ophthalmic artery sometimes entered the orbit to anastomose with the ciliary artery; but even when it occurs it is small and incidental. The whole of the orbit and eye is therefore supplied from the external carotid as well as the greater part of the circulation of the brain.

Among Ungulates, in the pig the circulation resembles that of the dog, but a well-formed rete is present supplied proximally by the ascending pharyngeal artery; it empties into a large trunk which is the only persistent portion of the internal carotid artery and contributes to the circle of Willis (Fig. 660). Arising from this last vessel there is a tenuous internal ophthalmic artery which anastomoses with the ciliary (Versari, 1900; Daniel *et al.*, 1953). In the sheep, goat, ox and horse, the external ophthalmic artery may arise directly from the internal maxillary, as it does in the dog, or from one of the group of vessels which form anastomotic channels through the carotid rete with the circle of Willis. As in the dog, a tenuous internal ophthalmic artery is present in the sheep and the goat but not in the ox. In the sheep and goat the rete is supplied wholly from the external carotid and, as occurs in the pig, the internal carotid only exists as an afferent vessel from this arterial network to the circle of Willis. In the ox and horse, however, an internal carotid vessel is present (Figs. 661–2) (Zietzschmann, 1913; Daniel *et al.*, 1953).

The orbital veins have not been fully worked out but in a general way they correspond with the arterial supply. In man, the greater part of the venous system returns into the intracranial system; in the lower Mammals the return is more and more to the extracranial system. In the rabbit the veins from the globe and orbit empty into an extensive ORBITAL SINUS which ramifies throughout the apex of the orbit,

enveloping the muscles and extending forwards to the level of the equator of the globe : its main exit channels are into the posterior and deep facial veins, the external and internal maxillary veins, and the vertebral vein (Davis, 1929).

The *orbital nerves* throughout the Placentals conform to the same general plan. The branches of the first division of the trigeminal serve as the sensory supply ; the sympathetic is vasomotor and innervates the smooth orbital muscle ; while the muscles are supplied by the IIIrd, IVth and VIth cranial nerves as in man except that the last nerve supplies the retractor bulbi muscle and the muscles controlling the nictitating membrane when these are present.

The CILIARY (ORBITAL) GANGLION is of interest. It is variable in nature but is always primarily associated with the IIIrd nerve. In the lower Fishes (Selachians, etc.) it is represented by groups of cells scattered along this nerve (H. Schneider, 1881 ; Pitzorno, 1913) ; in Teleosteans, Amphibians and Reptiles the ganglion becomes a specific entity associated with this nerve, usually without connection with the Vth or sympathetic (Schwalbe, 1879). In Birds it has a short root from the IIIrd nerve and a slender long root from the trigeminal (Lenhossék, 1911 ; Carpenter, 1911). Langendorff (1900) and Lodato (1900) were unable to confirm the nicotine reaction for the motor fibres in Birds ; it thus appears that physiologically as well as anatomically the cells in these animals are cerebro-spinal in type. It will be remembered that the ciliary muscle of Birds is striated. In Mammals, although it is small in Equidæ (Mobilio, 1912), the ciliary ganglion is always present, and in them the connection with the IIIrd nerve is always retained (Schwalbe, 1879 ; Peschel, 1893 ; Apolant, 1896). In many of them the root from the Vth nerve is absent, and frequently, when it is present, it conducts fibres of passage which are not relayed (Antonelli, 1890 ; Michel, 1894). The sympathetic root is more frequently absent ; and both of these roots may be absent in man. Among Mammals the ciliary ganglion is often represented by more than one group of cells.¹ It is probable that in many cases some of these different colonies of cells represent outgrowths of III and others outgrowths of V. When the ganglion is painted with nicotine the motor path is blocked, showing that this is mediated by cell-stations of the autonomic type (Langley and Anderson, 1892), while the sensitivity of the cornea remains unimpaired, showing that the sensory fibres are relayed in cell-stations which (if present) are of the cerebro-spinal type.

The ocular adnexa of aquatic Placentals deserve a special note. Some are only partially adapted to this medium. In the hippopotamus the orbits (like the nose) are elevated so that the eyes are readily kept above the water-level, the lids form a ring rather than a slit-shaped palpebral aperture, the lashes are sparse, and naso-lacrimal canals are lacking. In the Pinnipedes (seals and walruses) the orbits are also directed somewhat upwards, there are no tarsal glands, the lacrimal glands (although large in the fœtus) are small in the adult and the harderian glands are enormously developed, secreting an abundance of

¹ Ox, Muck (1815) ; rabbit, d'Erichia (1895), Mobilio (1912) ; pig, Antonelli (1890).

an oily substance to protect the keratinized cornea against the sea-water ; in the absence of naso-lacrimal canals, this secretion pours copiously over the face when the animal is on land (Fig. 663). In Sirenians (sea-cows) the lashes are extremely scanty but the lids freely mobile, closing completely over the small eye when it is pulled backwards by the well-developed retractor muscle. There is no lacrimal gland but the harderian gland is well developed, as in Pinnipedes, secreting a copious thick mucoid secretion like egg-white (Fig. 664).

The Cetaceans (whales and dolphins) are completely adapted to aquatic life : the lids are small, without tarsal plates or tarsal glands ;

FIGS. 663 AND 664.—AQUATIC PLACENTALS.

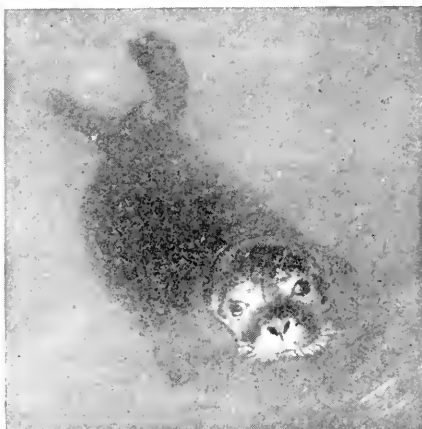


FIG. 663.—The Common Seal, *Phoca vitulina*.

Showing the upwardly directed eyes, as an adaptation for swimming (Zool. Soc., London).



FIG. 664.—The Head of the Manatee, *Trichechus manatus*.

Showing the small retractable eyes (photograph by Michael Soley).

lashes are lacking ; a “lacrimal” gland is present but secretes not tears but a fatty water-repellant secretion, and the same hypertrophy of the harderian gland is seen, the oily secretion of which is augmented by that of numerous oil-glands distributed over the palpebral conjunctiva. The naso-lacrimal conducting mechanism is absent as also is the nictitating membrane. The extra-ocular muscles are, however, enormous, more in keeping with the size of the animal than that of the small eye : each rectus is comparable to the biceps of man. In the whale this seems curious in view of the immobility of the downward-looking eye fixed firmly on its immensely rigid accessory optic nerve sheath and situated low down on a level with the angle of the mouth about one-third of the length of the huge animal away from its anterior extremity. It has been said that the enormous

muscles might be of value in keeping the eye warm by their tonic contraction in deep diving into the icy-cold ocean depths since here the thick layer of oily fat which insulates the rest of the body is absent ; but such a function is questionable. It would seem rather that, as in the elephant, the muscles have retained a size compatible with that of the animal while the globe has not.

For monographs on the study of the eyes of particular species, see :

Rodents—rabbit, Davis (1929) ; chinchilla, Detwiler (1949) ; mouse, Schwarz (1935) ;

Ungulates—okapi, Brückner (1950) ;

Carnivores—dog, Arey *et al.* (1942) ;

Primates—*Nycticebus*, *Nyctipithecus*, Detwiler (1939–41) ; apes, Hotta (1906).

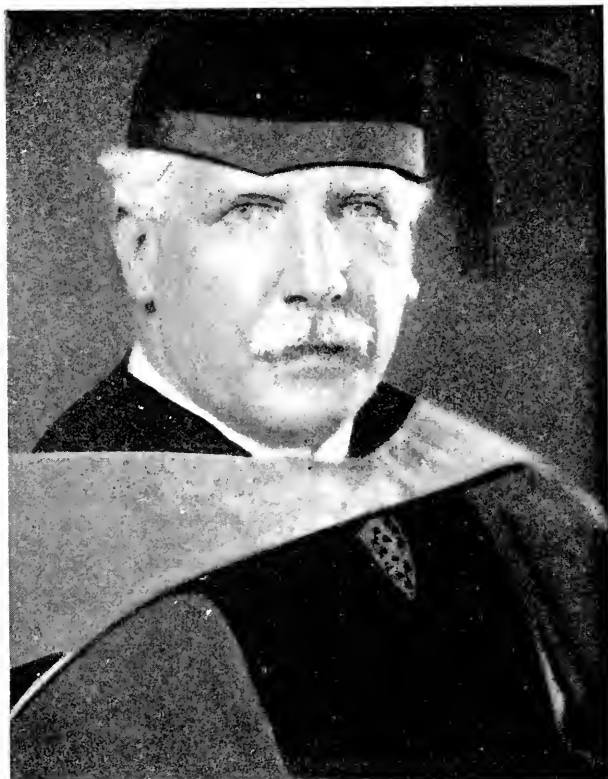
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C. U. Ariens Kappers

FIG. 665.—CORNELIUS UBBO ARIENS KAPPERS (1877-1946).

CHAPTER XVI

THE CENTRAL ORGANIZATION OF VISION

A consideration of the phylogenetic evolution of the central nervous organization of vision is suitably introduced by a photograph of CORNELIUS UBBO ARIËNS KAPPERS (1877–1946) (Fig. 665), Director of the Centraal Instituut voor Hersenonderzoek in Amsterdam in 1909, and Professor of Neuro-anatomy at the University of Amsterdam in 1928. In his generation he was the greatest authority on the comparative structure of the nervous system, and his magnum opus, *Die vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen* (1920), still remains the classical work on this subject. His work was not alone concerned with the factual description of structure but was enlivened and coordinated by much original thought. Among his speculative concepts the best known is that of "neurobiotaxis," a hypothesis by which he endeavoured to explain the complicated migration of nerve centres and tracts in phylogenetic history, and the seemingly peculiar location and relation in which this has resulted in the higher animals. This suggestion, that the final arrangement of neural elements is determined by an association of function, perhaps on a physico-chemical basis, is seen in many of those parts of the central nervous system which are associated with visual and photostatic functions—the position, for example, of the ocular motor nuclei in close relation to the posterior longitudinal bundle and the vestibular system, their secondary changes in position running parallel to changes in the paths of the optic, vestibular and coordinative reflexes, or the gradual development of a decussation of fibres at the chiasma so that fibres from regions of the retinae which work together run in contiguity.

In the first chapters of this book we have seen that light has a four-fold action upon living organisms—upon the general metabolism including the reproductive cycle, upon the control of movement, upon the retinal and integumentary pigmentation, and upon behaviour, and eventually consciousness, through visual sensations. In the more primitive animals the first two assume the greatest importance, in the higher the last becomes completely dominant, while the third always plays a somewhat subsidiary role. It is obvious, however, that none of these can become effective unless the local effects of the photochemical reaction initiated by light are made available to the organism as a whole and coordinated with its general activities. For this purpose two mechanisms are available—in the first the effects of the stimulus are conveyed by chemical means, in the second by nervous conduction.

The problems of communication and coordination were relatively simple in unicellular organisms, but unless evolution were not to pass beyond the stage of colonial Protozoa or the sponges and confine itself to entities comprised of loosely aggregated and relatively independent cells, rapidity of communication and control became essential for the development of a multicellular body with all its potentialities of specialization in structure and function. The evolution of an efficient conducting mechanism was thus

a necessity at an early stage if an organism were to combine large size with mobility and reactivity—attributes necessary for its survival. Even in unicellular organisms, however, a foretaste of two fundamentally different methods of response to light or other stimuli is evident—the first and most primitive, a simple quantitative *kinetic response* the mechanism of which is essentially chemical, and the other, a more qualitative *shock-reaction* the basis of which is electrical.

In the kinetic response the amount of light absorbed by a photosensitive substance determines a proportional increase or decrease of activity, a change which may be transmitted beyond the confines of the cell by the spread of the chemical products of the reaction. In the shock-response, the *rate of change* in the amount of light absorbed by the photosensitive tissue is of importance; the precarious electro-chemical balance of protoplasm in cellular form is maintained until the strength of the stimulus is sufficient to fire it into sudden activity, like an explosive, by a trigger-action. The first type of reaction is seen in plants and is typically evident as a regulator of basic activities in animals; the second is characteristic of the animal world and is seen in the lower organisms in their orientation to light and in the higher is typical of the economy of nervous activity.

The classical distinction between plants and animals as given, for example, by Haldane and Huxley in their standard work on biology as the only valid differentiation, concerned the type of foodstuffs they utilized, in the first case derived innocently from the air and the soil, in the second, from the syntheses accomplished by other living things. With some exceptions, such as insectivorous orchids, this is true, although difficulties arise among unicellular organisms on the border-line between plants and animals; thus some Flagellates have green chromatophores, others are colourless and live saprophytically and may be regarded as the starting point on the one hand of unicellular Thallophytes, on the other of Protozoa. A more fundamental differentiation, however, lies in the mechanism of their response to stimuli, a differentiation which determines the relative simplicity and serenity of vegetable existence with its close affinity to the sun's energy and the earth's chemistry, in contrast with the complexity and hurry-scurry of animal life with its mobility and independence.

In both plants (Blaauw, 1914–15) and animals (Northrop and Loeb, 1923) the stimulatory mechanism is purely photochemical, but there is a fundamental difference in the manner of conduction and in the effector mechanism. It is probable that all living cells are able to conduct waves of excitation, the common mechanism both in plant and animal cells being a wave of depolarization which passes along the plasma membrane and momentarily increases its permeability. But in plants the stimulus must be received directly by each cell, and propagation of the stimulus to a point at a distance is effected, not by the direct transmission of an impulse from cell to cell, but by the transfer of the products of the primary change, photochemical or otherwise, by a process somewhat more rapid than simple diffusion.¹ Such stimulatory substances have an obvious analogy to the products of the endocrine glands of animals but none to the propagation of nervous impulses. We have seen that substances of this type are responsible for the flowering of plants² and that a group of hormones, particularly the auxins, are responsible for the growth and movement of plants—substances which

¹ 10 mm. per hour in the case of auxin, p. 39.

² p. 10.

³ p. 39.

can diffuse through or can be trapped in gelatine and thus can be transferred to another plant, therein to produce the typical response. The experiments of Ricca (1916) on the highly irritable *Mimosa pudica*, or of Mangold (1923) on insectivorous plants, bring out the same point ; although the later investigations of Bose and Das (1925), Bose (1926-28) and Molisch (1929) would seem to indicate that in these very highly specialized forms many of the characteristics of nervous activity may be closely simulated. The difference, however, between the primitive response to light in plants and animals is merely a difference of method ; the reaction is fundamentally the same, the transformation of a photochemical change into a motorial response.

THE NERVOUS CONTROL

Although hormonal control persists in animals, particularly in the regulation of their basic activities, their movements and responses to external stimuli are active rather than passive : the explosive response fired by "trigger-action" gives them mobility. Even in the most primitive animals the energy provided by the photochemical reaction contributes to the chemical activation of neighbouring molecules, thus kindling a chain of chemical changes by means of which a phase of excitation is propagated through the protoplasm from the site of stimulation to the site wherein the response is produced. It is interesting that in organisms as lowly as Protozoa, differentiated fibrils are evident formed by basal granules arranged in longitudinal rows within the single cell, one at least of the functions of which is to coordinate the movements of the cilia (Neresheimer, 1903 ; Gelei, 1935). The evidence is convincing that some of these are paths for the propagation of stimuli, since microdissection experiments have shown that when they are cut the rhythm of the movements of cilia is disrupted (Taylor, 1920-41 ; MacDougall, 1928 ; MacLennan, 1935). There is also evidence that in colonial Protozoa, conduction can in this way proceed from cell to cell by intercellular fibrils (Taylor, 1941) (Fig. 666). In these forms this phenomenon is too rapid to be due to diffusion and too slow to have an electrical basis, and it is probable that these fibrils result from the preservation through natural selection of chance molecular patterns in the protoplasm which favour the relay of a train of chemical reactions, and that from these strand-like plastids nervous tissue, with its specialization as a conductor, had its origin (Bovie, 1926).

Once an effective intracellular means of conduction has been established, the obvious method of advance is for part of a cell to stretch and become specialized. In this way certain of the surface cells which, because of their exposed position receive stimuli from the environment, send long processes inwards conveying the message of their stimulation to neighbouring parts of the organism. Eventually, stretching many times their own breadth, they leave the surface layer and, abandoning sensory reception, specialize in conducting the excitations of other cells so that finally a network of conducting paths is laid down underneath the integument and the entire

FIGS. 666 TO 670.—THE EVOLUTION OF THE NERVOUS SYSTEM.



FIG. 666.—Two individuals of a protozoan colony joined by inter-cellular bridges.

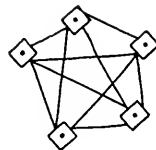


FIG. 667.—The impossibility of a direct cell-to-cell link in a complex multicellular organism. Five cells require 10 two-way channels.

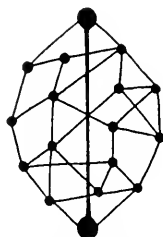


FIG. 668.—The nerve-net—a common network linking up all the cells with a trunk pathway between two important cells.

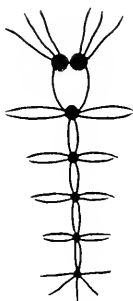


FIG. 669.—The ganglionic nervous system of Arthropods.

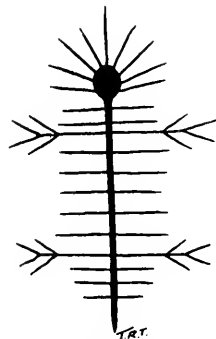


FIG. 670.—The central nervous system of Primates.

organism becomes coordinated in its response to a single stimulus. Thus a nervous system was born. A SUBEPITHELIAL NERVE-NET of this type made its first appearance in Coelenterates, but it is obvious that a diffuse network without short-circuiting and centralization is both wasteful and inefficient. Fig. 667 shows that to link up a large number of cells in this way becomes a practical impossibility : to link up 5 requires 10 two-way interconnections ; the most that can reasonably be done is to send out a call of general awareness. It has been a commonplace to compare the nervous system with a telegraphic exchange ; if any single subscriber is to be put in contact with any other economically, cables rather than a multiplicity of individual wires

must be employed and central exchanges must be introduced. And so the diffuse network became canalized into TRUNK-PATHWAYS between important parts—a stage reached in Echinoderms—and then telephone exchanges were introduced in the form of GANGLIA which are characteristic of the nervous system of the worms, Arthropods and Molluses ; therein not only the relay but the integration of messages became possible (Figs. 668–9). All through this process the head-end of the animal tended most readily to encounter external stimuli; in this region which first made the acquaintance of predators or prey, the sense-organs became concentrated. All through the process the degree of nervous development depended on the richness of the stimuli provided by the sensory organs—at first the tactile, chemical and olfactory,

FIGS. 671–2.—CONTRACTILE MYO-EPITHELIAL CELLS.

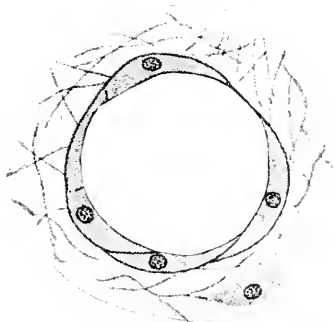


FIG. 671.—In the sponge, *Sycon gelatinosum*, the myo-epithelial cells surround the central aperture, which is capable of being contracted or dilated.



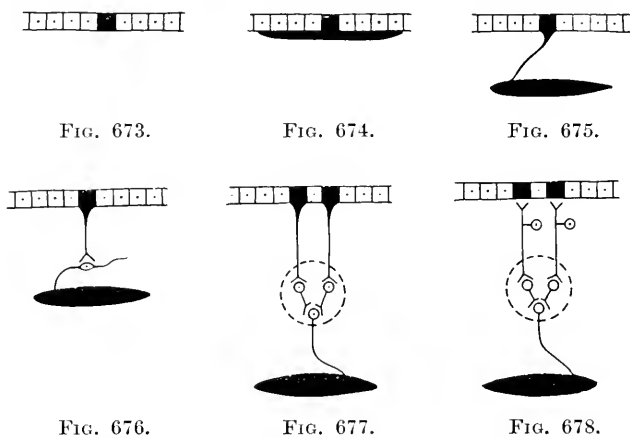
FIG. 672.—An isolated cell from the Coelenterate, *Pelagia*, showing the flagellum and the long striated muscular base (after Krasinska).

but eventually the visual ; and so at the head-end became concentrated the main exchange-centre which in course of time assumed control of all the others for the common good. This process of centralization resulted in the final development of the brain of Vertebrates (Fig. 670). To achieve this final development the whole of the economy of the body has been subordinated; on the supremacy of the main cerebral centre the eventual predominance of the Vertebrates and of man is built ; and in the end the evolution of vision is determined not by increasing specialization of the eye but on progressively more efficient analysis and integration by the cerebrum. "The law of progress is this—the race is not to the swift, nor to the strong, but to the wise" (Gaskell, 1908).

In Protozoa extracellular conducting nervous tissue was, in general, not required ; in the sponges (Porifera) no nervous elements exist, for these loose aggregations of cells with little community-life and without observable cohesion can be torn in pieces and reassemble again. These organisms thus exhibit none of the rapid reactions characteristic of the higher forms

of animal life, but at the same time they show a contractile response to tactile stimuli as their oscula open and close with movements of the seawater. This is effected by the evolution of contractile MYO-EPITHELIAL CELLS, epithelial cells which acquire the power to contract when stimulated and thus act as combined receptors and effectors; in higher forms these specialize in their contractile function and are displaced to form a muscular layer beneath the epithelium (Figs. 671 and 672). In Parker's (1911-18) view these muscular "independent effectors" are thus more primitive than nerve cells. Nor, indeed, is this illogical, for since all primitive responses

FIGS. 673 TO 678.—THE EVOLUTION OF RECEPTORS AND EFFECTORS.



- FIG. 673.—A specialized sensory cell (sponge).
 FIG. 674.—A myo-epithelial cell (an independent receptor-effector) (jellyfish).
 FIG. 675.—A receptor-effector system consisting of a sensory cell with a "nerve" fibril leading to a motor effector (muscle) (sea-anemone).
 FIG. 676.—The subepithelial nerve-net (jellyfish).
 FIG. 677.—An intercalary neurone between the receptor and effector (worms).
 FIG. 678.—A sensory organ, an afferent nerve (posterior root ganglion), an intercalary neurone and an effector organ (Mammals).

are tropisms, neither an independent receptor nor a conductor would be of value were a muscular effector not available. Initially the sense-muscle cell was stimulated directly; only when the muscle became specialized would specific receptors and conductors become necessary (Figs. 673 to 678).

THE NERVE-NET

In the Cœlenterates, the first type of animal to require a wholly coordinated body, a nervous system first made its appearance as a diffuse nerve-net,¹ lying between the epithelial layer and the subepithelial muscular layer. Into it dip down nerve-like processes from the sensitive epithelial

¹ For the physiological mechanism of the nerve-net, see Romanes (1876-77), Bethe (1903), Mayer (1908), v. Uexküll (1909), Parker (1917-32), Pantin (1935-52), Prosser (general review) (1939).

cells which establish relays with ganglion cells which have migrated inwards from the surface layer and have formed an interlacing network ; through these the underlying muscular layer is stimulated (Figs. 679 and 680). The early histologists pictured such a net as a syncytium composed of anastomosing fibres (Hadzi, 1909), but vital staining shows that the fibres run parallel to and intertwine with each other without actual fusion (Bozler, 1927 ; Woollard and Harpman, 1939) ; the junctions, however, are not polarized as in true synapses. Conduction, therefore, is free and equal in all directions so that any stimulus is diffusely spread (Eimer, 1874 ; Romanes, 1876) ;

FIGS. 679 AND 680.—THE SUBEPITHELIAL NERVE-NET OF CœLENTERATES.

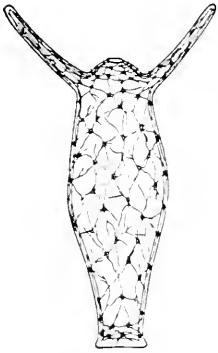


FIG. 679.—The nerve-net of *Hydra* (after Clause, Grobben and Kühn).

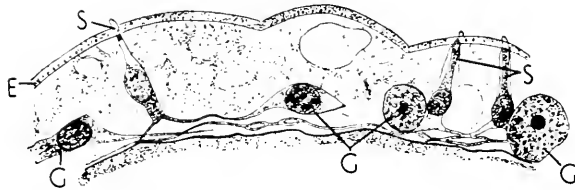


FIG. 680.—Subepidermal nerve-net around the oral disc of *Hydra*.

E, epidermis ; G, ganglion cells in the nerve-net ; S, epithelial sensory cells (after Hadzi).

consequently if interdigitating incisions are made and the animal is cut into zig-zag strips leaving only nervous connections, impulses pass either way and round corners so that an effective response is obtained.¹ Indeed, if all the sense-organs but one are removed from a jellyfish, the rhythmic impulses for swimming movements are started by the sole survivor and proceed in all directions. Control is thus entirely peripheral and execution indiscriminate without evidence of central integration, and to any stimulus the response is monotonously similar and universal.

While peripheral control by such a subepidermal nerve-net is the sole mechanism available to Cœlenterates, it persists in many animal groups—Echinoderms, worms (Fig. 681), Molluscs, and Balanoglossids—and finds an analogy in the autonomous visceral plexuses of Vertebrates such as the myenteric plexus which coordinates movements of the intestine. As evolution proceeds, however, the nerve-net assumes a more and more subsidiary role. The only area in turbellarian worms wherein the primitive

¹ Jellyfish—Mayer (1908) ; sea-anemone—Parker (1917) ; colonial Cœlenterates—Parker (1920).

complete independence is retained is in the proboscis, which, if nervously isolated, amputates itself and shows independent food-seeking reactions (Kepner and Rich, 1918). In Annelids and Molluscs, however, the nerve-net serves only as a relay system over a local area without independent activity, dealing with messages from the nerve-cord or ganglia. In general, the peripheral system is the more important in sluggish animals but as rapidity of response and general activity increase, the central mechanism takes over an increasing share of control.

Even in Coelenterates, however, some early signs of specialization are seen within the nerve-net. In some medusae and sea-anemones, through-tracts of long continuous fibres form nerve-trunks for rapid conduction,¹ and in sea-anemones a difference in the response between the free and the central end of a cut tentacle indicates a primitive type of polarity (Parker, 1917; Pantin, 1935). Moreover, the possibility of the existence of crude reflex arcs is indicated by the reciprocal contraction of circular and radial muscles (Bozler, 1926).

TRUNK-PATHWAYS

Although a hint of preferential conduction appears in Coelenterates, the advantage is obvious of short-circuiting the diffuse and indiscriminate conduction in a nerve-net through trunk-pathways composed of long giant fibres by which the transmission of vital messages between important points is rapid and direct; this is first achieved in Echinoderms in which radial symmetry has been attained. In the starfish, for example, there is a diffuse nerve-net, but from the sensory organs—the important olfactory and statolith organs and the yet unimportant eyes—situated at the tips of each of the five arms where the animal first contacts the dangers or opportunities of its environment, there arises a large nerve-trunk which runs down to the centre of the body where the five trunks combine to form a ring encircling the oral aperture (Fig. 166). This central nerve-ring with its five radiating nerve-trunks acts as the main directive system without which the animal shows sluggish and poor coordination in such activities as righting movements (Cole, 1913); at the same time these main pathways are linked closely with the peripheral net, which even in isolation can effect a certain amount of coordination, particularly by local reflexes between neighbouring spines (Langeloh, 1937; Smith, 1937–50; Kinoshita, 1941). At this stage central control is neither fixed nor complete but there is a plastic reciprocity between it and the still important peripheral system. It is probably for this reason that the starfish, although showing considerable complexity in behaviour in such reactions as feeding, righting itself, or escaping from restricted confines, yet shows no ability to profit by experience by adopting persistent modifications in its conduct (Jennings, 1907). Indeed, the animal may pull itself apart by the antagonistic activity of its own tube-feet

¹ *Callinectes*, in which the velocity of the contractile wave is 1.2 m./sec., compared with 0.15 m./sec. in the nerve-net (Pantin, 1935). In the nerves of the cat it is 119 m./sec.

(Kerkut, 1954-55). The primitiveness of the central coordinative control at this stage may best be illustrated by the analogy used by von Uexküll (1897) : when a dog runs the animal uses its legs ; when a sea-urchin runs the spines move the animal.

As evolution proceeds, we shall see that nerve-nets with directive conducting trunks get progressively less important in worms, Arthropods and Molluscs ; but it is of interest that the most primitive Proto-chordates, the Balanoglossids (Hemichordata), have a comparable non-integrated system of dorsal and ventral nerve-cords with collar-connections associated with a peripheral nerve-net (Bullock, 1940). It will be remembered ¹ that these worm-like burrowing creatures are without eyes. It is of interest that this primitive type of nervous system is an indication of the great phylogenetic age of the emergence of the chordate stock².

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THE GANGLIONIC NERVOUS SYSTEM

When bilateral symmetry was gained (as in worms) a further great advance in neural economy became possible, for now the sensory organs, the food-and-danger predictors gathered preferentially at the anterior end of the animal, led to a concentration of nerve-elements here also, thus inaugu-

¹ p. 227.

² p. 233.

rating the centralization of the nervous system. In this way the enormous economic benefit of central exchanges became possible, at first with one or more trunk-pathways running from the dorsal head-ganglion down the length of the body, and then as segmentation of the body progressed, with the interposition of ganglia in the central chain, each ganglion gathering up and issuing incoming sensory and outgoing motor nerves to its own particular segment. Within and between the segmental ganglia the incoming and outgoing nerves combined with associated neurones in the central system itself to form a complicated interconnecting network, the NEUROPILE, on which reflex activity could be built ; by means of these neurones which have no direct connection with the exterior, in association with the giant fibres of the trunk-pathways, the activities of the whole organism are coordinated, a foretaste of the infinitely complex system which finally constitutes the cerebral cortex of the Primates. In this way peripheral control through the subepidermal nerve-net gave place to central control through reflex pathways and the way was prepared for the dominance of cephalic sense-organs and nerve-centres, an arrangement seen in the nervous systems of worms, Arthropods and Molluscs.

THE NERVOUS SYSTEM OF WORMS

The initial stage in the development of the ganglionic nervous system is thus the appearance of a single cephalic ganglion from which issues a number of nerve-trunks which break up into the peripheral nerve-net. This

FIGS. 681 AND 682.—THE NERVOUS SYSTEM OF UNSEGMENTED WORMS.

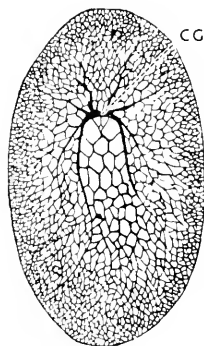


FIG. 681.—The nervous system of a primitive turbellarian worm.

Consisting of a cerebral ganglion, *CG*, with several nerve trunks and a subepidermal nerve-net.

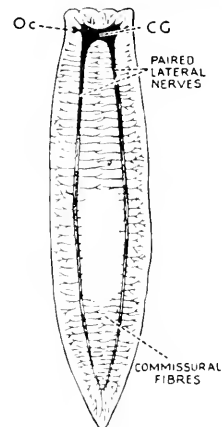


FIG. 682.—The nervous system of a higher type of turbellarian worm.

The fused cerebral ganglion, *CG*, with two closely associated ocelli, *Oc*, and paired nerve-trunks (after Hatchesek and Stempel).

is seen in the simplest unsegmented worms, such as some Turbellarians, wherein this single ganglion is responsible for relaying sensory messages and coordinating motor responses (Fig. 681). In other Turbellarians, two to eight nerve-cords run posteriorly from the ganglion (Fig. 682); each contains nerve cells, not yet grouped into ganglia, and gathers afferent fibres; and so long as these are left intact—but only so long—spontaneous movement and coordinated responses persist.¹ When the rudimentary ocelli are few they are grouped on the dorsal aspect of the anterior end and the nerve fibres run directly into the cerebral ganglion; when they are many and diffusely scattered, they enter the peripheral nerve-net. The former arrangement is also seen in the larvæ of some Insects (Fig. 683).

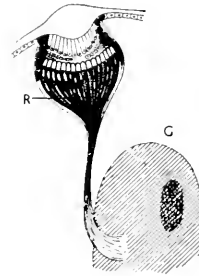


FIG. 683.—THE EYE OF THE LARVA OF *ACILIUS*.

The fibre-like prolongations of the light-sensitive cells, *R*, go directly into the cerebral ganglion, *G* (after Gaskell).

Again, the simple system of a single ganglion controlling a peripheral mechanism is seen among the primitive Protochordates in the Tunicates; when the ganglion is removed the Ascidian may slowly develop reflexes confined to a single siphon when stimulated, but all inter-siphonal responses and general coordination are lost (Kinoshita, 1910; Day, 1919; Prosser, 1946).

In SEGMENTED WORMS (ANNELIDS), however, the nerve-cells are grouped into ganglia, each subserving the receptor-effector mechanism of its own and often adjacent segments. The simplest form of such a system is seen in Oligochaetes such as the earthworm, *Lumbricus* (Fig. 684). Situated dorsally in the third segment are two cerebral ganglia from which emerge two nerve-cords; initially these form a ring around the pharynx beneath which

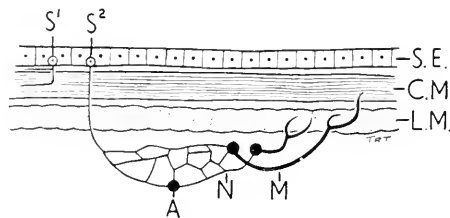


FIG. 684.—NERVOUS SYSTEM OF A SEGMENTED WORM.

Transverse section through the earthworm. *S.E.*, surface epithelium; *C.M.*, circular muscles; *L.M.*, longitudinal muscle; *S¹*, sensory cell the fibre from which terminates directly in the subepidermal nerve-net; *S²*, sensory cell the fibre from which goes to a segmental ganglion to merge in the neuropile; *A*, association neurone, the processes from which do not leave the central nervous system but run mainly up and down the ganglionic chain (perpendicular to the page); *M*, two motor neurones, the dendrites of which contribute to the neuropile; *N*, neuropile, composed of processes of the three types of cell—sensory, motor and associative.

¹ Bardeen (1901) in Planarians; Eggers (1924) and Friedrich (1932) in Nemertines; Rietschel (1935) in Cestodes.

they unite as the first ventral ganglion and then run to the posterior extremity of the body to form a double but compact united ventral nerve-cord. The segments are short and the segmental paired ganglia which connect with the subepidermal nerve plexus are almost confluent; and down the nerve-cord there run three dorsal and two ventral giant fibres which transmit impulses down the entire length of the worm, mediating rapid

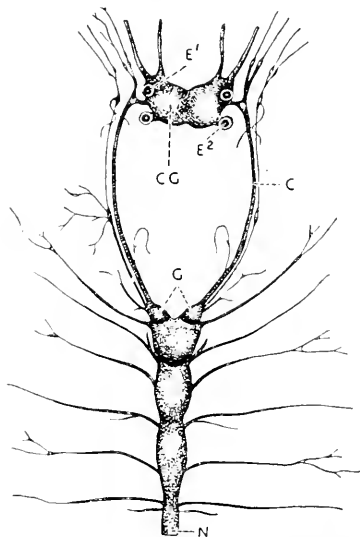


FIG. 685.—THE NERVOUS SYSTEM OF THE POLYCHAETE WORM, *NEREIS*.

CG, cerebral (supra-oesophageal) ganglion, in close association with which are the 4 eyes—a paired anterior, E^1 , and posterior, E^2 . The infra-oesophageal ganglion, G, marks the beginning of the ganglionated nerve cord, N, connected to the cerebral ganglion by circum-oesophageal connectives, C (after Quatrefages).

direction of the response is reversed; if the ventral cord is sectioned the anterior part of the animal turns away from the light, the posterior towards it (Hess, 1924; Nomura, 1926–27; Prosser, 1934; Howell, 1939). The negative responses are thus controlled by the brain, the positive by the ventral cord. The activity of the cerebral ganglion therefore normally dominates that of the lower ganglia, the responses of which it normally opposes. After the cerebral ganglion is removed from the earthworm, the animal remains active, eats, burrows and copulates, the reactions, however, being performed some 10 or 15 times more slowly (30 as compared with 2 minutes); a similar decrease in responses is induced by subnormal temperatures or depressive drugs. The same operation in *Nereis*, on the other hand, leaves it overactive in its responses to

end-to-end “startle” reactions (Stough, 1926–30; Smallwood and Holmes, 1927; Bullock, 1945).¹ The peripheral nerve-plexus is largely a sensory relay, and although occasional connections² between sense organs directly to the underlying muscle may persist, they are unimportant in behaviour over which the central nerve-cord has taken complete control (Janzen, 1931; Coonfield, 1932; Prosser, 1935; and others).

In the polychaete worms, the segmentation becomes more obvious: the well-formed cerebral ganglion, the oesophageal ring and the commencement of the ventral ganglionated cord of *Nereis* are seen in Fig. 685. The bi-lobed cerebral ganglion, which resembles structurally the cerebral ganglion of Arthropods, receives nerves from the tentacles and palpi as well as the short, thick optic nerves from the four simple eyes which seem almost to be sitting upon it.

The progress of cephalic dominance in the segmented worms is interesting. Normally, the earthworm is negatively phototactic to light, but after removal of the cerebral ganglion the

¹ The speed of travel in the giant fibres is 17 to 45 m./sec., whereas that in the small fibres of the cord is 0.025 m./sec. (Bovard, 1918; Eccles *et al.*, 1933; Bullock, 1945).

² None recorded in the Polychaetes (Just, 1924).

light or chemical stimuli but unable to burrow. If the subœsophageal ganglion is then removed, the worm lies quiet and inert (Loeb, 1894 ; Maxwell, 1897 ; Prosser, 1934). It would thus seem that the cerebral ganglion is primarily a sensory centre exercising an inhibitory control upon the motor centres in the subœsophageal ganglion. One of the main functions of the brain is thus anticipated. In the group of worms, we therefore see the disappearance of peripheral independence, the establishment of central control and the beginning of cerebral dominance.

THE NERVOUS SYSTEM OF ARTHROPODS

THE ARTHROPOD NERVOUS SYSTEM is built on the same plan as that of the polychæte worms. In Crustaceans, such as the crayfish (*Astacus*) and in Insects there is a bi-lobed cerebral ganglion receiving sensory nerves from the eyes and the first two antennæ which contain the organs of smell, hearing, taste and equilibration ; this connects by the circum-œsophageal nerve-ring with the fused and ganglionated ventral nerve-cord in which run giant fibres as well as associated neurones (Fig. 686). In some of the smaller Crustaceans and the Onychophora (*Peripatus*) the two nerve-cords are widely separated. On the other hand, in many of the higher Insects such as flies (Diptera) several consecutive ganglia of the ventral nerve-cord are fused (Figs. 687-91) ; in crabs (Decapoda), sessile barnacles (Cirripedia), spiders (Araneida) and bugs (Hemiptera) the fusion is complete so that the ventral ganglia form a single mass (Figs. 688, 691). Moreover the higher Crustaceans and Insects possess a simple visceral or sympathetic system connected with the circum-œsophageal ring, which passes backwards on the alimentary canal.

The optic lobes and cerebral ganglion of Arthropods are illustrated in Figs. 692 to 696. The cerebral ganglion consists of three fused segments forming one mass : (1) the PROTOCEREBRUM or optic segment forming the greater part of the brain and receiving nerves from the compound eyes and ocelli, (2) the DEUTEROCEREBRUM derived from the antennary segment, and (3) the TRITOCEREBRUM from the third segment of the head which supplies the region of the mouth. The whole structure contains a peripheral layer of ganglion cells with a central mass of neuropile containing several groups of associative cells forming the CENTRAL BODY, the PEDUNCULATE BODIES and other smaller accumulations of cells ; these are comparatively large in social insects and are generally regarded as regulating behaviour.



FIG. 686.—THE NERVOUS SYSTEM OF A TYPICAL CRUSTACEAN.

CG, cerebral (supra-œsophageal) ganglia ; OR, circum-œsophageal nerve ring ; SA, sternal artery running between a separation of the two ventral nerve-cords ; SOG, sub-œsophageal ganglion (consisting of 6 pairs of fused ganglia) ; G, a pair of fused ganglia of the ventral cord (after Thomson).

THE EYE IN EVOLUTION

FIGS. 687 TO 691.—THE NERVOUS SYSTEM OF INSECTS.



FIG. 687.



FIG. 688.

FIG. 687.—The nervous system of the larval stage of Lepidoptera (caterpillar). Note the cerebral (supra-oesophageal) ganglia connected with the sub-oesophageal ganglion by the circum-oesophageal nerve ring and the chain of ganglia of the ventral cord.

FIG. 688.—The nervous system of Hemiptera (water-bug). The ganglia of the ventral cord are fused into one.



FIG. 689.

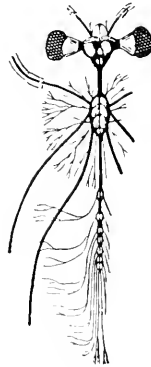


FIG. 690.

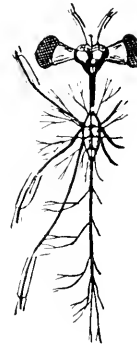


FIG. 691.

FIGS. 689 to 691.—The nervous system of diptera, showing the general arrangement of the cerebral and sub-oesophageal ganglia closely approximated and the thoracic and abdominal ganglia of the ventral chain. On either side of the cerebral ganglion the enormous optic lobes and compound eyes project laterally, each larger than the ganglion itself (modified from Lang).

FIG. 689.—*Chironomus*, with three thoracic and six small abdominal ganglia.

FIG. 690.—*Tabanus*, with one (fused) thoracic ganglion and seven abdominal ganglia closely approximated.

FIG. 691.—*Sarcophaga*, with all the thoracic and abdominal ganglia of the ventral chain united in one mass.

On either side of the protocerebrum there emerge the relatively enormous OPTIC LOBES contained in eye-stalks which bear the compound eyes. The reconstructed eye-stalk of the fresh-water crayfish, *Cambarus*, is seen in Fig. 692 (Fernhards, 1916 ; Welsh, 1941). Herein several neuropile masses form optic ganglia ; of these, as a general rule in Crustaceans and Insects,

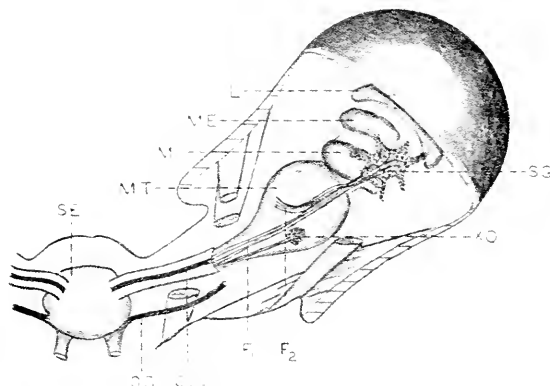
FIGS. 692 AND 693.—THE RIGHT EYE-STALK OF THE CRAYFISH, *CAMBARUS*.


FIG. 692.—The dissected eye-stalk, with the cuticular covering and the sheath enveloping the optic lobes removed.

*F*₁, fibre tract from supra-oesophageal ganglion to sinus gland; *F*₂, fibre tract from medulla terminalis to sinus gland; *L*, lamina ganglionaris (optic ganglion I); *ME*, medulla externa (optic ganglion II); *MT*, medulla interna (optic ganglion III); *MT*, medulla terminalis (optic ganglion IV); *OC*₁, oculomotor nerve I; *OC*₂, oculomotor nerve II; *SE*, supra-oesophageal (cerebral) ganglion; *SG*, sinus gland; *XO*, x-organ (*J. H. Welsh, J. exp. Zool.*).

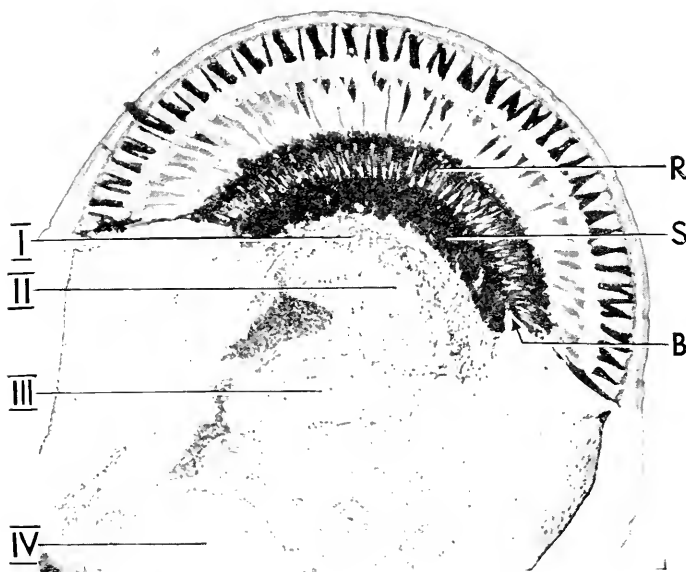


FIG. 693.—Section through the eye-stalk.

On top is the compound eye with the retinal cells, *R*, at the proximal end of the ommatidia. The sub-ocular space, *S*, is occupied largely by pigment and between it and the retinules is the basement membrane, *B*. Occupying the main body of the stalk are the four optic ganglia, I to IV (lamina ganglionaris, external and internal medullae, and the medulla terminalis) (*Norman Ashton*).

there are three—the LAMINA GANGLIONARIS (or first optic ganglion), the EXTERNAL MEDULLA (or second optic ganglion) and the INTERNAL MEDULLA (or third optic ganglion) which is frequently divided into two or more parts. In some Decapods there are two, while in others, as the crayfish, *Cambarus*, there are four, a TERMINAL MEDULLA (or fourth optic ganglion) lying proximal to the third. The fibres from the visual cells of the compound eye enter the first optic ganglion directly; between the ganglia there are two well-marked decussations of fibres, and from the proximal ganglion the afferent fibres enter the cerebral ganglion by several tracts to terminate in the primary optic association areas, particularly the pedunculate body, and to decussate over to the opposite side. Removal of the cellular portion of the pedunculate body abolishes certain responses to light (Bethe, 1897).

From the ocelli (when they are present) the visual fibres end in a ganglion just proximal to the eye wherein a second neurone enters the protocerebrum and after making connections with the fibres from the optic lobes, seeks the visual centres (Fig. 696)¹.

From the optic centres fibres pass downwards through the circum-oesophageal commissures into the thoracic cord. These fibres have been divided into two systems by Satija (1957) (Fig. 696): several ipsilateral fibre-tracts pass downwards from each optic ganglion into the commissure on the same side while a single large fibre, also arising from each optic ganglion, crosses in the midline to enter the contralateral commissure. On visual stimulation action potentials have been recorded along their route (Parry, 1947; Burt and Catton, 1952–54) and they presumably link up the visual stimuli with the reflexes mediated by the nerve cord.

It is interesting that the brain of Insects is large in those with the more complex behaviour; thus that of *Dytiscus* is 1/400 of the body-volume, of the bee 1/174 (Wigglesworth, 1953). Moreover, the size of the visual centres varies similarly with the degree of development of the eyes. In Arachnids and Myriapods with simple eyes the visual centres are some 0.3 to 2.8% of the size of the brain; in Crustaceans and Insects with rudimentary compound eyes, it is 3 to 10%; in those with elaborate compound eyes, up to 80% (Hanström, 1928).

It is noteworthy that synchronized spontaneous rhythms resembling those of the vertebrate brain have been found in the ganglia of Arthropods and Molluscs, indicating a considerable degree of coordination and a high level of excitability in the constituent neurones.² This type of activity, it will be remembered, is characteristic of integrative centres and absent in those with purely distributive and sensory functions.

In function, the cerebral ganglion of Arthropods plays a decisive role in the animal's conduct. Apart from its essential purpose as a receiving

¹ For the structure of the nervous system of Arthropods, see Cajal (1918), Snodgrass (1926), Hanström (1928–35), Ehnborn (1948); for the action-potentials in the optic ganglia on stimulation by light, see Adrian (1937) in the water-beetle, *Dytiscus*; Crescitelli and Jahn (1942), Bernhard (1942), Burt and Catton (1956), in the grasshopper, *Chortippus*; Autrum (1950), Burt and Catton (1956), in the blowfly, *Calliphora*; and Burt and Catton (1954–56), in the locust, *Locusta migratoria*, and the larva of the dragon-fly, *Aeschna*.

² The water-beetle, *Dytiscus*—Adrian (1937); the grasshopper, *Chortippus*—Crescitelli and Jahn (1942); the slug, *Ariolimax*—Bullock (1945); the blowfly, *Calliphora*—Burkhardt (1954); the locust, *Locusta migratoria*—Burt and Catton (1956).

centre for optical and other sensations from the sense organs concentrated in the head, it acts as an association centre and exercises an important integrative, particularly inhibitory, control over motor activity throughout the body. This is well seen in ablation experiments. After removal of this ganglion either in Crustaceans or Insects, spontaneous locomotion and coordinated feeding cease but local segmental reflexes persist, and owing to the removal of inhibition these activities tend to be much exaggerated, whether they control reflex movements, locomotion or the chromatophores. Section of one circum-oesophageal connective leads to unilateral effects and circus movements (Jordan, 1918 ; Herter, 1931 ; ten Cate, 1931 ; Prosser, 1946). This inhibitory action of the cerebral ganglion over the ventral

FIGS. 694 TO 695.—THE OPTIC LOBES AND CEREBRAL TRACTS OF THE INSECT.

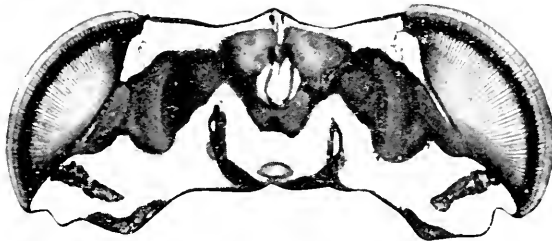


FIG. 694.—Vertical section through the head of a bee.

Showing, centrally, the paired protocerebrum or cerebral ganglion, underneath which are the sub-oesophageal ganglia. Joining the compound eye with the central nervous system lie the optic lobes wherein the three nuclei—the lamina ganglionaris externally, the external medulla and internal medulla internally—are well differentiated (Norman Aslinton).

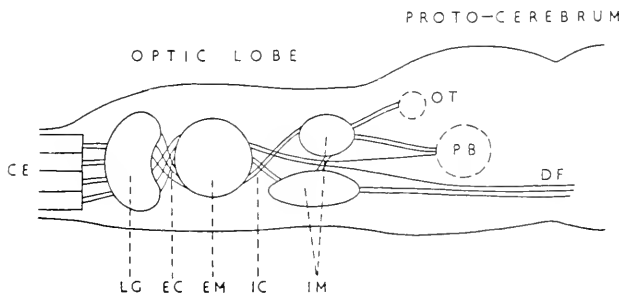


FIG. 695.—Scheme of the visual paths from the eye to the protocerebrum in a typical insect.

CE, compound eye, from which nerve fibres go directly to the lamina ganglionaris (optic ganglion I), LG. Thence a decussation of fibres, the external chiasma, EC, leads to the external medulla (optic ganglion II), EM. Thence a third relay of fibres, the internal chiasma, IC, leads to the internal medulla (optic ganglion III), IM, which may be divided into two parts. Thence fibres are relayed to the optic centres in the cerebral ganglion—mainly the optic tubercle, OT, and the pedunculate body, PB—as well as contributing decussating fibres, DF, to the nuclei of the other side. For the descending fibres, see Fig. 696.

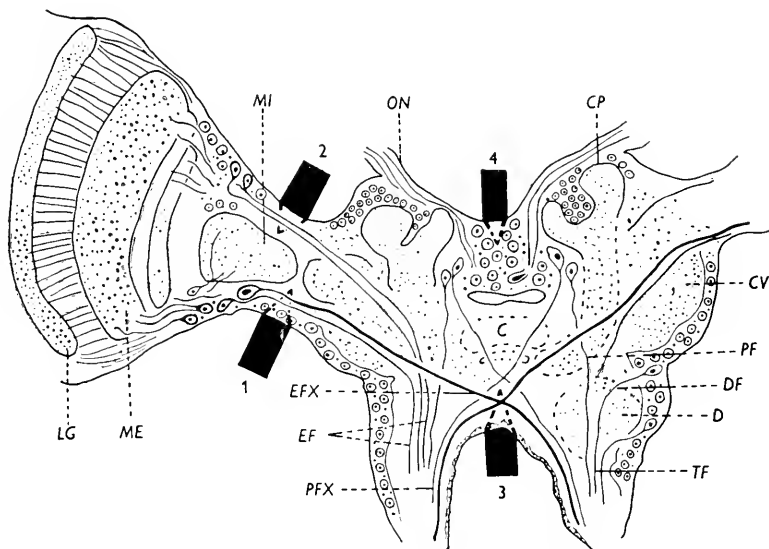


FIG. 696.—FRONTAL SECTION OF THE CEREBRAL GANGLION AND OPTIC LOBES OF THE LOCUST, *LOCUSTA*.

Showing descending tracts to the nerve cord (reconstructed). C, central body; CP, corpora pedunculata; CV, corpora ventralia; D, deutocerebrum; DF, descending tract from deutocerebrum; EF and EFX, ipsilateral and contralateral fibres from optic lobes; LG, lamina ganglionaris; ME, external medulla; MI, internal medulla; ON, ocellar nerve; PF and PFX, ipsilateral and contralateral fibres from corpora pedunculata; TF, descending tract from tritocerebrum.

With the incisions indicated by numbered black pointers, the following effects on the visual responses were noted: 1, in the ventral region and posterior aspect of the optic peduncle, the crossed responses were abolished; 2, on the dorsal and anterior aspect of the optic peduncle, the ipsilateral responses were weaker; 3, between the two halves of the protocerebrum ventrally, the crossed responses were abolished bilaterally; 4, between the two halves of the protocerebrum dorsally, no effects on the visual responses were found (R. C. Satija, *J. Physiol.*).

ganglia was well demonstrated by Jordan (1910) who showed in the crab that the circus movements ceased if the cut end of the connective were electrically stimulated.

The exaggeration of reflex reactions after removal of the cerebral ganglion is seen in the elicitation of responses to stimuli normally without effect and the continuation of movements (such as cleaning movements of the legs) uninterruptedly for hours (Bethe, 1897; Roeder, 1937; and others). In decapitated females of *Bombyx*, oviposition can be induced mechanically before mating and persists until all the eggs have been laid, merely by pressing the ovipositor (McCracken, 1907); the same type of response is seen in the stinging reflex of the bee (v. Buddenbrock, 1937). In the same way when the female praying mantis devours her doomed mate head-first, his copulatory activity increases manifold in violence and apparent enthusiasm when she has disposed of his cerebral and sub-oesophageal ganglia (Roeder, 1935).

The activities of Arthropods are essentially reflex in nature, controlled with amazing precision by the ganglionic centres; when the eye of the

locust is stimulated by light, for example, impulses have been recorded as far caudally as the last thoracic ganglion (Bütt and Catton, 1952). Nevertheless, these ganglia do not act merely as automatic relay-stations. As we have already seen ¹ disturbances of the normal mechanism of locomotion by the amputation of a limb are largely corrected by suitable alterations in the reflex progression (Bethe, 1930 ; v. Holst, 1935 ; ten Cate, 1936 ; and others). Moreover, within the nerve-cord, the available connections are multiple and after experimental interference it has been shown that the choice of a particular pathway depends on such factors as the strength of stimulus and the ease of transmission (Prosser, 1935. in the crayfish). In view of the complexity of the instinctive behaviour, particularly of Insects, as exemplified in the complicated social behaviour of the ant or the dance of the honey-bee by which it indicates to its fellows the location of a honey-store,² and in view of their limited but very definite capacity to modify their behaviour by learning and conditioning, it would seem that the ganglionic organization of Arthropods with its cerebral dominance has reached a very high level indeed of integration. It must be remembered, however, that despite their complexity and seemingly intelligent basis, these complex patterns of behaviour are all innate and their performance depends on the development of the appropriate parts of the nervous system or, in the case of sexual instincts, on the development of hormones at a somewhat later stage in life. Even although their behaviour does seem often elaborate and sometimes full of intelligence, however, individual adjustment to any peculiar circumstances is relatively unknown in their totalitarian lives ; individuality and personality cannot be attained below the level of a centralized brain.

THE NERVOUS SYSTEM OF MOLLUSCS

In MOLLUSCS which are unsegmented and without appendages, the nervous system appears to be different but nevertheless is basically similar to that of worms and Arthropods. In its essentials it consists of paired dorsal cephalic ganglia which receive sensory fibres from the eyes and other sense-organs ; these ganglia are connected by a short circum-oesophageal nerve-ring with paired pleural and pedal ganglia. Typically, as an offshoot from this bunched-up ganglionated ring in the head-region, a stomatogastric loop from the cerebral ganglia runs below the gullet bearing two buccal ganglia, and a visceral loop provided with visceral ganglia is given off from the pleurals (Fig. 697). In some types the ganglia in the cephalic ring are separate (Gastropods), in others they are so closely associated that some appear to be fused (cerebro-pleural in Lamellibranchs), while in Cephalopods the fusion is almost complete. In these last the three pairs of ganglia are crowded into the head region around the oesophagus so closely that their

¹ p. 59.

² p. 70.

boundaries are appreciated with difficulty (cerebral, pedal and pleuro-visceral), all being well protected by investing cartilages.

In the Cephalopods, the sub-oesophageal ganglionic mass contains centres for regulating the locomotor and visceral activities; here lie the centres which control the ocular muscles, the pupil and the chromatophores. To the supra-oesophageal (cerebral) ganglia come the sensory efferents, here lie the higher motor centres controlling movements of large groups of muscles, and here also, situated in the upper part of the ganglion, lies a large associative and integrative area, ablation of which does not impair purely reflex

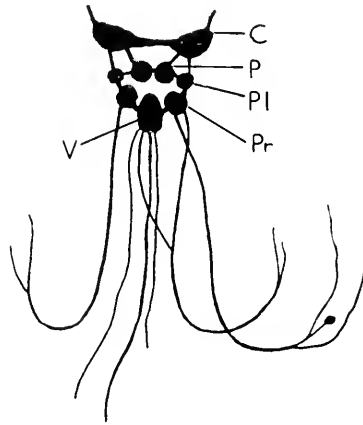


FIG. 697.—THE NERVOUS SYSTEM OF A PULMONATE MOLLUSC, *LIMNÆA*.

A pair of cerebral ganglia, C, overlie the oesophagus, below which is a mass of ganglia composed of 2 pedal ganglia, P, 2 pleural, Pl, and 2 parietal, Pr, while ventrally in the centre lies the visceral ganglion, V (after Spengel).

activities or sensory impressions but abolishes initiative in behaviour and plasticity in responses; this is seen, for example, in such reactions as chasing prey round blind corners or in attempting expedients to escape from artificial restrictions (*Sepia*, *Octopus*—Buytendijk, 1933; Sanders and Young, 1940).

The course of the nerve-fibres associated with vision is shown in Fig. 698.¹ The axons of the retinal ganglion cells leave the eye, decussate in the very short optic nerve and enter the large optic lobes situated one on either side of the paired cerebral ganglion which they dominate completely by their size. Around the periphery of the optic lobe run two layers of granular cells separated by a plexiform layer of fibres, while in the centre of the lobe are two nuclei, a central and a peduncular nucleus. The axons of the ganglion cells of the retina enter the plexiform layer between the two granular layers and here they meet dendrites of these cells; the pathway is

¹ For the anatomy of the visual fibres of Molluscs, see v. Uexküll (1895), Cajal (1917), Kappers et al. (1936), and Sanders and Young (1940).

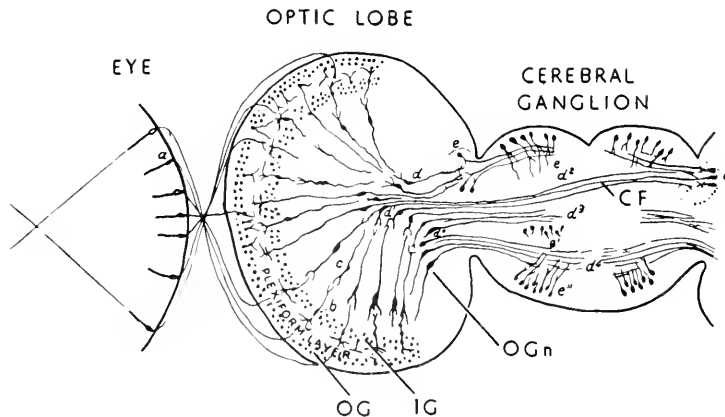


FIG. 698.—DIAGRAMMATIC SCHEME OF THE VISUAL PATHS AND THEIR CENTRAL CONNECTIONS IN THE CEPHALOPOD (after Kappers).

Axons from the visual cells in the compound eye, *a*, decussate to form a chiasma and enter the optic lobe, terminating in the plexiform layer between the inner, IG, and outer granular layers, OG. The pathway is continued by axons of the granular cells, *b*, sometimes with an intercalated neurone, *c*, to the central and pedunculate nuclei of the optic ganglion, OGn. Thence a further relay, *d*¹ to *d*², continues the pathway to the cerebral ganglia to terminate in association areas, *e*, and, by means of commissural fibres, CF, in the contralateral optic lobe.

continued by the granular cells, sometimes with an intercalated neurone, to a central mass of cells, the optic ganglion, consisting mainly of a central and a peduncular nucleus; from this a fourth relay enters the cerebral ganglion to terminate in association areas anteriorly and posteriorly and to decussate to the optic lobe on the other side. It is noteworthy that the large and complex optic lobes (in the octopus) serve as the centres for learning to attack objects that provide food, a demonstration of the effective role vision plays in this essential activity; thence fibres pass to the cerebral ganglion where are situated the cells responsible for initiating attack-behaviour (Young, 1953).

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THE CENTRAL NERVOUS SYSTEM

A central nervous system is characteristic of the Chordates which possess a brain and dorsal nerve-cord replacing the cerebral ganglion and the ventral cord of the Invertebrates, the whole being initially supported by a notochord and eventually encased in a protective bony skull and vertebral column. In the Proto-chordates, however, the nervous system is exceedingly primitive.

We have already seen ¹ that in the HEMICHORDATES (*Balanoglossus*) the nervous system is essentially a peripheral nerve-net centred round a dorsal nerve-cord arising as a longitudinal groove of ectoderm connected by a band around the collar of the animal with a ventral nerve. There is as yet no evidence of a brain. In larval TUNICATES there is a poorly developed ganglionic brain connected with the median eye and continued in a dorsal nerve-cord ²; but in the sessile adult Ascidian the nervous system recedes until it is represented merely by a single ganglionic mass from which a few short nerve-filaments emerge.³ In the ACRANIA, the brain of *Amphioxus* (*Branchiostoma*) is almost undeveloped and is represented by a small cerebral vesicle, but the dorsal cord with its central canal is well formed and sends off two anterior cerebral nerves and a pair of segmental nerves, dorsal and ventral, to each myotome (Fig. 236).

Among VERTEBRATES the central nervous system attains a structural complexity and functional coordination unparalleled in the animal kingdom,

¹ p. 227.² p. 228.³ p. 228.

until eventually it acquires a plasticity and adaptability sufficient to form a structural basis for the physical dexterity and intellectual supremacy of man. In contrast with the types of nervous system we have just discussed, the activities of which are expressed in simple and immediate reflexes concerned with the ready transformation of afferent impulses into somewhat stereotyped responses, it makes provision to an increasing degree for the appreciation of broadly correlated sensory patterns, for individual adjust-

FIGS. 699 TO 702.—THE EVOLUTION OF THE BRAIN OF VERTEBRATES.

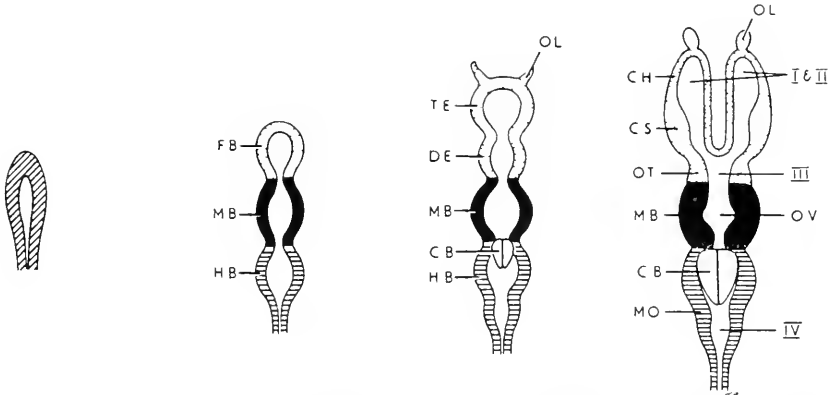


FIG. 699.—The initial archencephalon; a vesicular-shaped swelling at the upper end of the medullary tube.

FIG. 700.—The stage of three primary cerebral vesicles.

FIG. 701.—The stage of five cerebral vesicles.

FIG. 702.—The final division of the telencephalon.

The fore-brain and its derivatives are dotted; the mid-brain is in solid black; the hind-brain is cross-hatched.

CB, cerebellum; *CH*, cerebral hemispheres; *CS*, corpus striatum; *DE*, diencephalon; *FB*, fore-brain (prosencephalon); *HB*, hind-brain (rhombencephalon), divided into metencephalon and myelencephalon in Figs. 701-2; *MB*, mid-brain (mesencephalon); *MO*, medulla oblongata; *OL*, olfactory lobe; *OT*, optic thalamus; *OV*, vesicle which becomes the iter or aqueduct of Sylvius; *TE*, telencephalon; I, II, III and IV, ventricles.

ments in response and eventually for the emergence of thought and personality. Within the Vertebrates, however, this process of evolution was slow but conformed to a general plan whereby the reflex mechanism in the lower levels became gradually subordinated to the controlling and integrating influence of a cerebral cortex. In the process, changes affecting the central visual mechanism played a predominating part, and the gradual transference of the sensory activities of vision to the highest level, leaving the reflex photostatic functions at a lower level, formed the pivot around which the nervous system of the higher Vertebrates eventually became reorganized.

As in the lower Chordates, the central nervous system of Vertebrates is formed from the dorsal ectoderm by the infolding of the medullary groove

to form an ectodermal tube enclosing an axial canal,¹ the anterior end of which dilates markedly to form the brain while the remainder forms the segmented dorsal spinal cord; the latter acts as a reflex centre, while in addition to this, the former assumes controlling and integrating functions of ever-increasing importance so that as evolution proceeds the entire mechanism shows a progressive degree of cephalization.

At an early period the embryonic cerebral vesicle shows two constrictions dividing it into three primary bulb-like vesicles—the FORE-BRAIN (PROSENCEPHALON), the MID-BRAIN (MESENCEPHALON) and the HIND-BRAIN (RHOMBENCEPHALON) (Figs. 699 to 709). During the course of vertebrate evolution these three primary vesicles differentiate as follows:

FORE-BRAIN	$\left\{ \begin{array}{l} \text{TELENCEPHALON—olfactory lobes, cerebral cortex (pallium), basal} \\ \text{nuclei of the corpus striatum.} \\ \text{DIENCEPHALON—thalamus, epithalamus, hypothalamus, epiphysis,} \\ \text{hypophysis.} \end{array} \right.$
MID-BRAIN	Tectum (and optic lobes or, in Mammals, corpora quadrigemina), tegmentum (and, in Mammals, cerebral peduncles).
HIND-BRAIN	$\left\{ \begin{array}{l} \text{METENCEPHALON—cerebellum and part of medulla oblongata (in} \\ \text{Mammals, the pons).} \\ \text{MYELENCEPHALON—remainder of the medulla oblongata.} \end{array} \right.$

In some fishes this division into five main segments is maintained, but in most Vertebrates the telencephalon grows out into two paired lobes (the cerebral hemispheres), each containing the cavity of a lateral ventricle (Fig. 702).

It is interesting that in Cyclostomes the histological structure of the central nervous system is extremely primitive and its organization allows for the most part only total movements of the whole body (mass reflexes) rather than complex adjustments involving precise coordination. It is thus unspecialized, plastic and capable of differentiation in any direction—a very suitable primordial ancestor for the Vertebrates (Herrick, 1921). The central nervous systems of selachian and teleostean Fishes, on the other hand, show systems of nuclei and fibre-tracts as well defined as those of Mammals; they are precisely adapted on a reflex plane to a particular environment, and although they are thus able completely to dominate this habitat, their central nervous systems are less capable of free adjustment to other conditions. They therefore form terminal branches of the phylogenetic tree.² The ancestors of the Amphibians were the more primitive Crossopterygii, nearly related to which are the lung-fishes (Dipnoi). Their more plastic central nervous system and the more complete evagination of the fore-brain into cerebral vesicles, particularly at the caudal rather than the olfactory end, allowed them to become adapted to the lessened oxygen supply in stagnant swamps and ultimately to emerge on land. On this relatively primitive fish-brain further evolution was therefore based.

We shall now outline the main evolutionary changes in the development of the brain of Vertebrates with particular reference to their visual systems (Figs. 700 to 715).

¹ p. 239.

² p. 234.

FIGS. 703 TO 709.—THE BRAINS OF VERTEBRATES
(after Bütschli, Gaupp, Crosby, Clark, Kuenzi and Sisson).

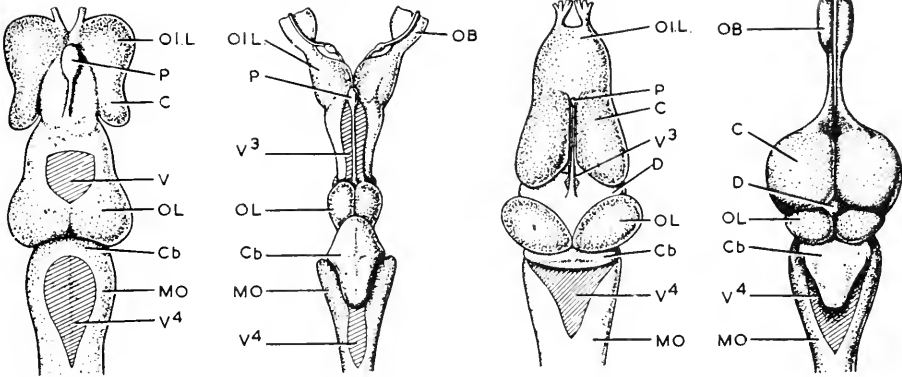


FIG. 703.—A Cyclostome: the lamprey, *Petromyzon*.

FIG. 704.—A Selachian: the shark, *Scymnus*.

FIG. 705.—An Amphibian: the frog, *Rana*.

FIG. 706.—A Reptile: the alligator.

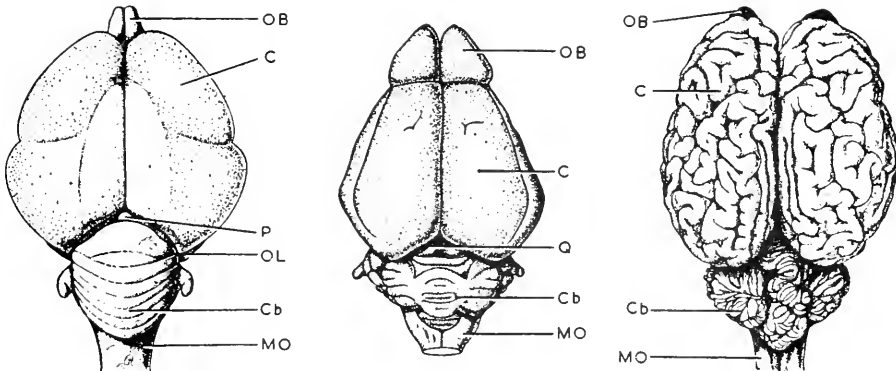


FIG. 707.—A Bird: the goose, *Anser*.

FIG. 708.—A lower Mammal: the Insectivore, *Gymnura*.

FIG. 709.—A higher Mammal: the horse, *Equus*.

C, cerebrum; Cb, cerebellum; D, diencephalon; MO, medulla oblongata; OB, olfactory bulb; OL, optic lobe; OIL, olfactory lobe; P, pineal complex; Q, corpora quadrigemina; V, ventricle of mid-brain; V³, third ventricle; V⁴, fourth ventricle.

The *hind-brain* essentially continues the segmental functions of the cord, acting as a reflex centre for most of the head-region through the cranial nerves, both sensory and motor, but in addition it assumes integrating functions for such general autonomic activities as circulation and respiration and the control of equilibration and posture. The last is subserved by vestibular centres upon which the cerebellum is built as an integrating centre, linking up the vestibular centres with the sensory organs mediating these

functions (the lateral lines ¹ and labyrinths ²) and associating them with fibres from the cord and the mid-brain, many of which are derived from the ocular muscles. In addition, in all Vertebrates the hind-brain receives the receptors of taste, and in the higher Vertebrates from Amphibia upwards, the auditory nerves. The cochlea, which makes its appearance first in Amphibia and is attuned to respond to the vibrations of the new medium (air), belongs to the same system of vibratory sense-organs as the lateral line and labyrinth.³

Initially the postural mechanism of the hind-brain was relatively self-sufficient ; thus after transection of the brain cephalad to the hind-brain, Cyclostomes, Fishes and Amphibians retain their locomotor functions, while in these animals the cerebellum is but poorly developed. In Reptiles, Deiters' nucleus first becomes important in immediate relation with the vestibular system, and in Birds and Mammals, the integrating and inhibitory functions of the higher centres become so overwhelming that transection at this level results in decerebrate rigidity so that independent locomotion becomes impossible, while ablation of the cerebellum results in the complete breakdown of equilibration.

The *mid-brain* contains the visual and oculomotor centres in the lower Vertebrates and acquires auditory centres in the higher ; it also acts as an integrating centre for proprioceptive and exteroceptive impulses, linking them by means of elaborate connections with the hind-brain and cerebellum and in an ever-increasing degree with the higher centres. The roof of the mid-brain (the TECTUM) has undergone profound changes in evolution (Figs. 710 to 715). Originally it received all the afferent fibres from the eyes which were primarily photostatic. In Cyclostomes the tectum is rudimentary and most of the incoming fibres are visual; from it issue tecto-bulbar tracts which bring the movements of the animal under the control of optic and other sensory impulses (Fig. 710). In Fishes this region becomes enormously expanded to form the two OPTIC LOBES, and in addition to optic fibres, it receives spino-tectal fibres conveying sensory impulses from the body, head and neck. In these animals the tectum thus serves not only as the visual centre but acts as the coordinating station for many motor and other sensory activities. In Amphibians, the differentiation of a system of receptors for the cochlea leads to the appearance of two separate centres on each side, one for the eye and one for the ear : the bigeminal body becomes the quadrigeminal. In the higher Vertebrates, the optic lobes are thus divided into four (the corpora quadrigemina) and while the anterior paired bodies (superior colliculi) receive visual, the posterior (inferior colliculi)

¹ Present in aquatic Vertebrates—Cyclostomes, Fishes, all urodele and larval anuran Amphibians ; when Vertebrates left the water for the land the lateral line disappeared.

² Present in all Vertebrates. In Myxinoids there is one semicircular canal, in other Cyclostomes, two (anterior and posterior), in other Vertebrates, three (anterior, posterior and external). The free opening of the labyrinth in some selachian fishes (dog-fish, *Acanthias* ; skate, *Raja*) indicates the analogy to lateral line organs.

³ The sacculus and papilla lagunæ of fishes may be sensitive to auditory vibrations (Piper, 1900 ; Parker, 1903-12).

receive auditory afferents. In Reptiles such as the lizard this area is thus an elaborate structure resembling that of Birds ; in the latter the tectal region reaches its highest peak of development and the superior colliculi themselves have attained the importance of *optic lobes with a cortex*, generally accepted as being arranged in six layers of nerve cells and fibres (Cajal, 1889 ; Huber and Crosby, 1929 ; Jungherr, 1945 ; Shirasu, 1953). The first (the stratum zonale) is a thin layer of flat small cells ; into the second (the stratum opticum) the optic fibres arrive to terminate in the third (the stratum griseum), itself divided into seven layers ; the remaining layers are concerned with the cells and fibres which form the efferent tracts from the

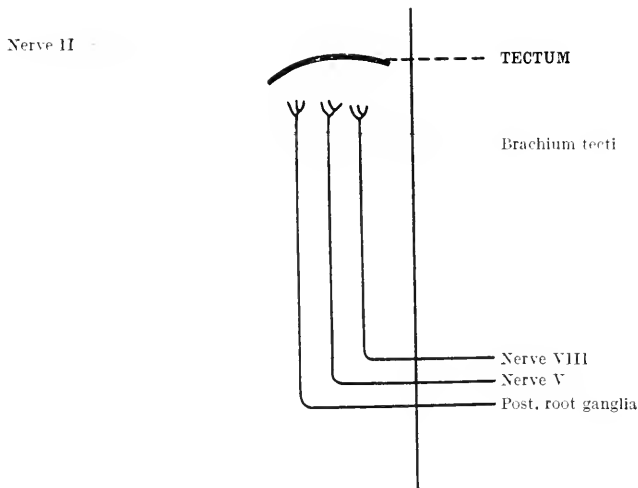


FIG. 710.—THE VISUAL PATHWAYS IN A TYPICAL CYCLOSTOME.

tectum. In Mammals, however, the importance of the optic lobes begins to decline ; the sensory fibres are relayed to a more plastic end-station in the cerebral cortex and the tectum eventually receives only the fibres associated with the primitive photostatic functions of vision.

The ventral portion of the mid-brain (the *TEGMENTUM*) contains the oculomotor nuclei and in the higher Vertebrates is concerned to an ever-increasing degree with the integration of fibre-systems from the general proprioceptive system and the octavus (VIIIth nerve) system with the higher centres, a function which, in Reptiles and above, is centred in the upper part of the mid-brain ; transection at the level of the red nucleus in Mammals thus leads to decerebrate rigidity.

In the lower Vertebrates (Cyclostomes, Fishes and Amphibians) the mid-brain is thus the region of the highest integration of their sensory and motor activities (apart from smell) and controls the most complex behaviour of these animals ; for this reason electrical stimulation leads to coordinated movements much as does stimulation of the cortex of Mammals. In Birds

the dorsal area of the mid-brain assumes immense importance as a correlating centre for sensory, gravistatic and photostatic impulses ; the fact that these correlations still take place at this level reflects the essentially reflex and instinctive nature of these animals with their poor adaptability and lack of potentiality for further evolution. In Mammals, however, the tectum fails to meet the demands of complex visual differentiations and pluri-sensory combinations, a shift upwards of the sensory centres to a higher level of greater plasticity is necessitated, and this region merely retains the regulation of restricted photostatic and other activities. In Mammals the

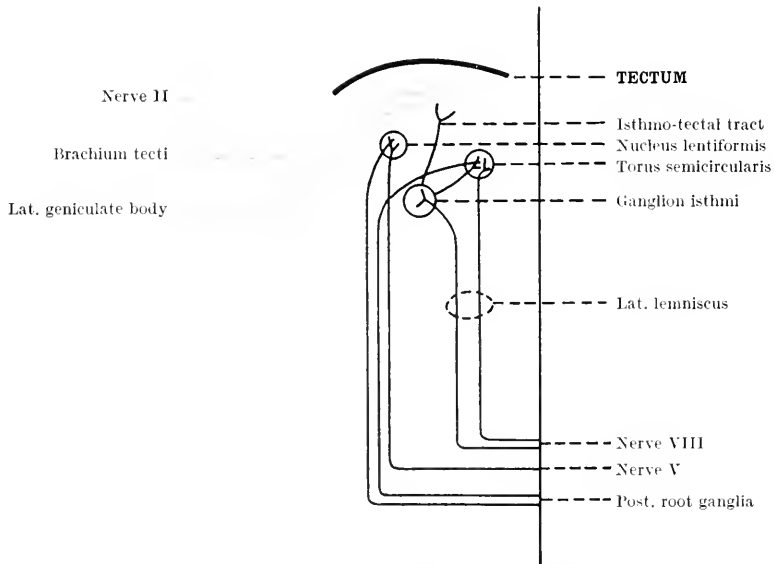


FIG. 711.—THE VISUAL PATHWAYS IN A TELEOSTEAN FISH.

anterior colliculi and tectum are therefore much reduced owing to the diversion of the mass of optic fibres to the lateral geniculate body. In the same manner, in the quest for more ample and effectual sensory associations, the inferior colliculi cease to be an end-station for hearing and serve merely as a relay-station to the cerebral cortex, but nevertheless they retain considerable importance in gravistasis as the main end-station of the lateral lemniscus (Nerve VIII) and the spino- and bulbo-mesencephalic fibres.

Destruction of the optic lobes in Fish and Amphibia is said to leave the vision normal provided the rest of the mid-brain is intact (Loeser, 1905) ; but in Birds, removal of the colliculi disturbs visual reflexes and produces virtual blindness (Marquis, 1935). On the other hand, in Mammals in which the visual fibres are relayed to the cortex, lesions of the colliculi or tectum give rise to no observable visual defect (rabbit, rat—Ghisla, 1937) ; such a lesion, moreover, does not affect the pupillary reflexes which are centred in the pretectal area (cat—Keller and Stewart, 1932 ; Magoun, 1935).

The *diencephalon*, where the central canal persists as the third ventricle, has peculiar visual and secretory functions in addition to the important integrative activities of the optic thalamus. From its ventro-lateral aspects in the embryo the primary optic vesicles which form the lateral eyes emerge as out-pouchings, and it is interesting that in many species there is evidence that the cells of this region, particularly those of the ependyma lining the ventricle, appear to retain some photosensory functions.

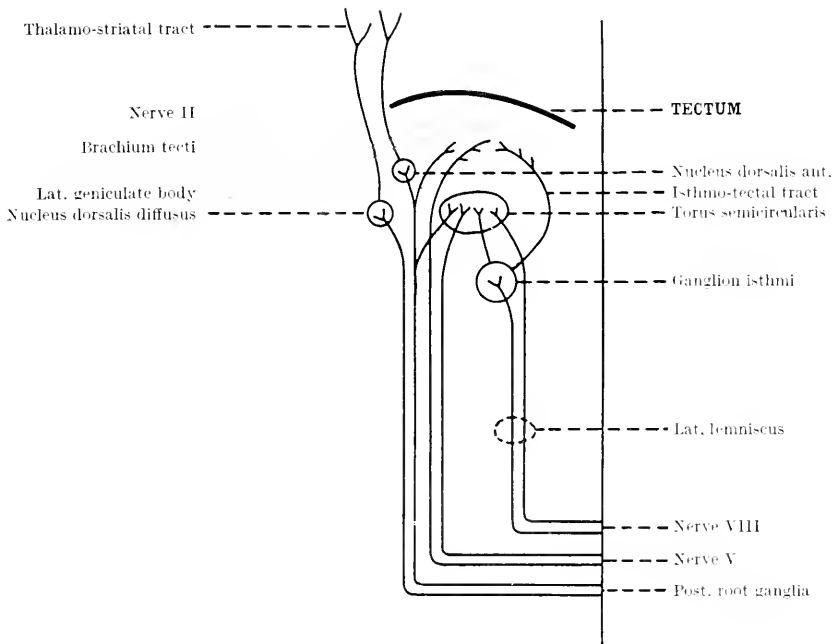


FIG. 712.—THE VISUAL PATHWAYS IN A TYPICAL AMPHIBIAN.

This direct photosensitivity of the central nervous system, especially the diencephalon, has been established in experiments on the action of light upon gonadotropic activities¹ and changes in the chromatophores of the integument in a number of species by several workers, notable among whom are von Frisch (1911) (fish), Scharrer (1928) (minnow), Nowikoff (1934), Young (1935) (lamprey), and Benoit (1937) (ducks). We have already seen that Benoit and his collaborators (1952-53) showed that the direct stimulation of this region by light enhances the gonadotropic activity of ducks from which both eyes had been removed; and Parker and his colleagues (1952) have pointed out that the central nervous system of most Birds and Mammals contains a coproporphyrin pigment with absorptive properties which could account for this direct photosensory response.

The secretory activities of the diencephalon are equally important.² From its thin roof which consists merely of a single layer of ependymal

¹ p. 16.

² p. 558.

cells reinforced by the choroidal plexus, is given off the pineal and in some Vertebrates (Cyclostomes, some Fish and Reptiles) the parietal organs ; in some lower Vertebrates these have an optical function but in the higher types the pineal body has only a glandular function.¹ From the floor a ventral process, the infundibulum, grows in front of the anterior extremity of the notochord to meet a diverticulum from the pharynx to form the pituitary gland (or hypophysis), and with it are associated a number of nuclei of neuro-secretory cells which not only control the potent endocrine products

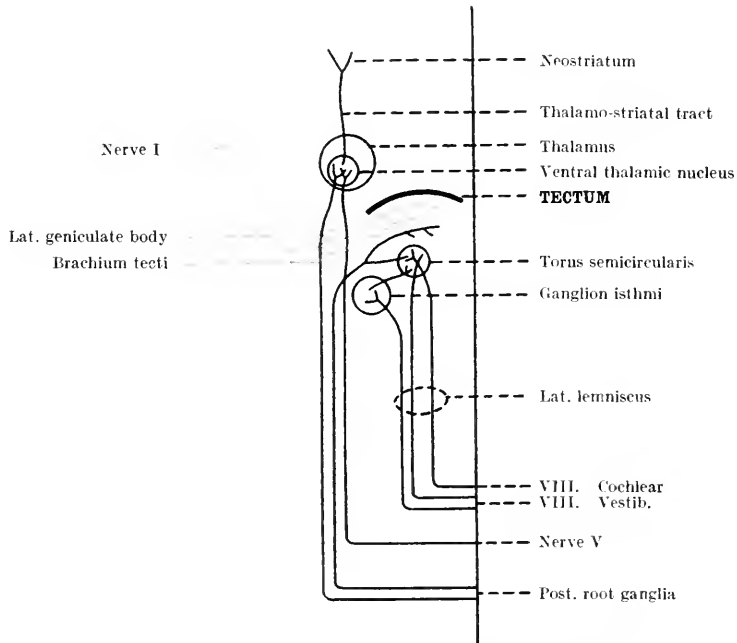


FIG. 713.—THE VISUAL PATHWAYS IN A TYPICAL REPTILE.

of the pituitary but, through it, exercise a governing influence over most of the endocrine system.²

The OPTIC THALAMUS when fully developed is a region of great integrative importance. Its more *dorsal nuclei* are concerned with widespread somatic sensory functions, the special senses and associative sensory functions. In Vertebrates below Mammalia it is the part of the brain which is responsible for the affective appreciation of experience and therefore, in the last resort, it determines behaviour ; the cerebral hemispheres merely form the receptive apparatus for olfactory impressions. In Mammals it is the principal end-station for all the sensory systems of the body with the exception of the olfactory projections which proceed directly to the cerebral cortex. In these

¹ p. 716.

² p. 558.

animals (dog, etc.) ablation of the thalamus leads to immediate blindness which, however, is soon replaced by psychical blindness only (Panizza, 1855); this demonstrates that a function resembling that of the cerebral cortex is still to some extent retained. In man its connections are of an extremely intricate kind since it forms the main relay-station of all the tracts spreading upwards towards the cortex. Those parts which are concerned particularly with the special senses are the lateral geniculate

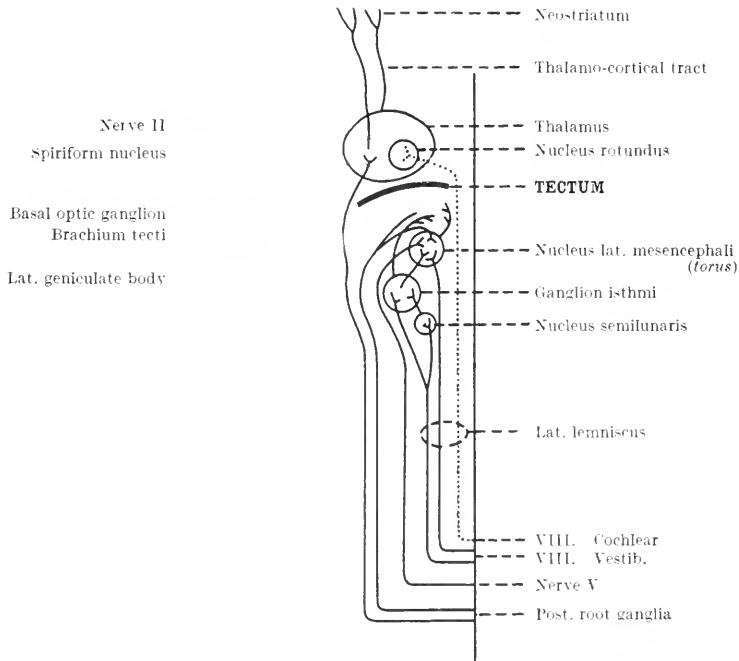


FIG. 714.—THE VISUAL PATHWAYS IN A TYPICAL BIRD.

bodies (vision) and the medial geniculate bodies (audition and possibly equilibration) while the pulvinar has indirect visual and auditory associations.

The *ventral part of the diencephalon* is occupied by the hypothalamus, a collection of nuclei with rich intra-diencephalic connections which in the higher Vertebrates are concerned with cardiac acceleration, elevation of the blood pressure, the maintenance of the intra-ocular pressure, pupillary dilatation, retraction of the nictitating membrane, pilo-erection, and inhibition of the gut, as well as such vegetative functions as the regulation of temperature, water, fat and carbohydrate metabolism, sleep and sexual activity.

The optic thalamus and its associated nuclei are primitive in Cyclostomes, being chiefly concerned with olfactory, visual and visceral sensory

responsibility for the integration of the very complex patterns of instinctive behaviour characteristic of the higher Vertebrates.

This is made clear by the researches of Brügger (1943), Hess and Brügger (1943) and Hess (1943-44). Probing the hypothalamic region of cats with electrodes, they found areas where the stimulus elicited complex patterns of behaviour in their entirety, such as fighting, eating and sleeping, all displayed in perfect coordination. Thus the cat looked around, searched for a suitable corner in which to go to sleep, and forthwith went to sleep; presumably felt hungry, searched for food, ate the food, rested, and so on. Here, therefore, lie the anatomical bases of the centres controlling the highest instinctive patterns, set between the receptors and effectors, combining and assessing incoming impressions and redispersing instructions in an integrated form, at the same time relaying on to the cortex those requiring further analysis. These thalamic centres control the lower centres and in higher animals are themselves influenced and controlled by higher cortical centres, an effect seen, for example, in the "sham rage" and evidences of general sympathetic hyperactivity that occur in the cat after its cortico-thalamic connections have been cut (Bard, 1928; Cannon, 1929).

The two nuclei derived from the thalamus with visual connections are the lateral geniculate body and the pulvinar.

THE LATERAL GENICULATE BODY. The anlage of the lateral geniculate body is evident even in the primitive Cyclostomes (Herrick and Obenchain, 1913); it is recognizable in most Fishes as a nest of cells in the angle between the optic tract and the tectum (Franz, 1912), and is relatively well developed in Teleosteans (Kappers, 1920). In Amphibians, Reptiles and Birds, it remains small (see Kappers, 1921) and is not projected onto the cortex (Elliot Smith, 1928), but in Mammals it shows an abrupt development. It is well represented among all Mammals except semi-blind types such as the mole (Ganser, 1882; Frankl-Hochwart, 1902), and it assumes many variations of structure in the different species.¹ In the more primitive Mammals (Marsupials) it has a dorsal and a ventral nucleus showing no lamination, and lies vertically on the surface of the brain (Fig. 715). The ventral nucleus is the more primitive and is homologous with the entire geniculate body of Fishes, Reptiles and Birds: the dorsal nucleus only is projected to the cortex.² As evolution proceeds, changes take place consisting of a disappearance of the primitive ventral nucleus, the appearance of rows of large cells along the periphery of the dorsal nucleus, and the lateral rotation of the whole structure so that the original external surface lies ventrally. Its highest differentiation is seen in the Primates, in which it is represented almost entirely by the dorsal nucleus.³ In these the primitive ventral nucleus has dwindled almost into insignificance; it probably receives only crossed optic fibres and none from the recently developed macula (Minkowski, 1920), and from it issues the brachium

¹ v. Monakow (1883), Cajal (1904), Sachs (1909), Neiding (1911), Winkler and Potter (1914), Horne-Craigie (1925), Overbosch (1926), Putnam (1926), Le Gros Clark and Penman (1934), Packer (1941), Le Gros Clark (1941).

² v. Monakow (1883), Kappers (1920), Winkler (1921), Brouwer (1923), Putnam (1926).

³ Ziehen (1903), Sachs (1909), Friedemann (1912), Minkowski (1913).

tecti ; it is related to the reflex centres in the mid-brain and has no connection with the cortex, persisting in man after lesions in the geniculo-calcarine path.¹ The ventral nucleus thus probably retains the primitive photostatic functions, while the higher visual functions are probably all taken over by the more lately differentiated dorsal nucleus with its elaborate laminated structure and point-to-point retinal representation² (Ingvar, 1923 ; Woollard, 1926 ; Le Gros Clark, 1941-42).

THE PULVINAR. This nucleus occupying the posterior extremity of the thalamus appears late in phylogenetic history, becoming of considerable size only in Primates in which its development may be correlated with the adoption of the erect posture. While undoubtedly associated with visual and auditory integrations, its connections with these systems are still obscure. It would appear to have no direct connections with the retina or the visual cortex, nor with the ascending somatic tracts (Minkowski, 1913 ; Brouwer and Zeeman, 1926) but projects to the parastriate area of the cortex (area 18) and to the posterior Sylvian receptive area adjacent to the auditory area

FIGS. 716 TO 718.—THE DEVELOPMENT OF THE TELEENCEPHALON.

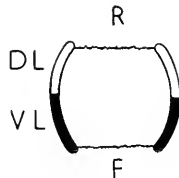


FIG. 716.

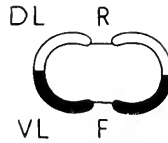


FIG. 717.

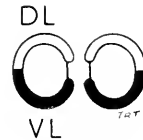


FIG. 718.

FIG. 716.—Initially the telencephalon appears as a tube with thick lateral walls of nervous tissue and a thin non-nervous roof, *R*, and floor, *F*. The lateral walls are divided into dorso-lateral, *DL*, and ventro-lateral, *VL*, segments.

FIG. 717.—During further development the lateral walls turn inwards leaving a narrow area representing the roof and floor.

FIG. 718.—The inturned dorsal and ventral edges of each lateral wall fuse, forming out of the unpaired vesicle two cerebral hemispheres, each containing a lateral ventricle. The dorso-lateral wall, *DL*, forms the cortex ; from the ventro-lateral wall, *VL*, develop the nuclei of the corpus striatum.

(area 22) (Le Gros Clark and Northfield, 1937). Its association with the cerebellum (Clarke and Horsley, 1905) and the red nucleus (Sachs, 1909) and with the thalamo-cortical fibres for the arm region in the precentral convolution of the brain may perhaps reflect the importance of the hand and fingers in Primates in exploration and manipulation, and the nucleus may act as an integrating area for the coordination of the eye and the hand, being thus related to the higher visual functions of stereognosis (Winkler, 1919 ; Kappers, 1920).

The *telencephalon* is present in all Vertebrates, the dorsal part of its lateral walls forming the cortex, the ventral walls the nuclei of the corpus striatum (Figs. 716 to 718). Initially it was built up as a receptor station for the olfactory nerves, and the dominance of the higher Vertebrates is essentially due to the replacement of the original palæocortex based upon the sense of smell by the neocortex built around the sense of vision.

¹ Brouwer (1917-26), Minkowski (1920), Winkler (1921), v. Monakow (1924).

² Id.

In Cyclostomes and Fishes the entire telencephalon and much of the diencephalon are devoted to olfactory activities. In Amphibians are seen the beginnings of the emergence of non-olfactory systems into this region of highest integration ; although no part of their cerebral hemispheres is free from olfactory connections, much of their thalamus is devoted to other sensory mechanisms, and it is significant that the first indication of a sensory cortical projection—the thalamo-cortical tract of Amphibians—is not visual (Rubaschkin, 1903 ; Herrick, 1917). In Reptiles the ascending sensory systems are greatly enlarged so that they monopolize areas of the corpus striatum and the cortex, while in Mammals the sensory and somatic systems dominate the cortex to an ever-increasing degree until in man the olfactory centres become insignificant and are relegated to an obscure corner while the visual projections are prolific and widespread.

In Cyclostomes and selachian Fishes the entire fore-brain is represented by an insignificant PALÆOCORTEX with purely olfactory functions, which persists as the pyriform lobes (the primary olfactory cortex) of the higher Vertebrates. To this is added in Teleosteans the ARCHICORTEX, still entirely olfactory, which persists as the hippocampus (the secondary olfactory cortex). It is interesting that in Cyclostomes, “ganoid” and teleostean Fishes the fore-brain has a non-nervous (ependymal) roof. In Amphibians some non-olfactory fibres reach the fore-brain and in Reptiles a TRUE CORTEX first appears. In Birds this structure is well developed and the olfactory lobes have become small ; but its surface is still smooth, the roof is still thin and its main mass is occupied by the relatively enormous corpus striatum. The neopallium as we know it is a characteristic of Mammals, serving as a receptor area of optic, auditory, tactile and other sensory stimuli, an initiator of voluntary movements and a centre for associative memory and eventually of conceptual thought. As the scale of mammalian evolution is ascended this portion of the cerebrum becomes increasingly important and the olfactory area less ; in Insectivores or the rabbit, for example, the cortex is only slightly convoluted and does not cover the cerebellum (Fig. 708) ; in the horse and the dog convolutions have become prominent (Fig. 709), while in the Primates both anatomically and functionally it has become the master-tissue wherein afferent sensory impressions are assessed and stored and are correlated through an intricate system of association fibres with the complex activities of these animals.

The *evolution of the visual pathways and centres* will be readily understood from this short sketch of the phylogenetic development of the brain (Figs. 710 to 715). In Cyclostomes (apart from the degenerate Myxinoids¹), the optic fibres from the retina are projected into the superficial layers of the tectum, here to come into relation with the bulbo- and spino-tectal fibres arriving to the deeper layers (Fig. 710) ; in these a primitive anlage of the lateral geniculate body may be present (Herrick and Obenchain, 1913). In Fishes a few collateral fibres are given to the still very rudimentary lateral

¹ p. 734.

geniculate bodies, while the optic axons again terminate in the tectum and its dorsal extensions, the optic lobes (Fig. 711). Here there is a point-to-point representation of the retina (Lubsen, 1921 ; Buser and Dusardier, 1953). In Amphibians the tectum is more highly differentiated, but still there is no higher projection of visual fibres (Fig. 712) ; in these and in Reptiles optic fibres terminate in the lateral geniculate body which emits only a geniculo-tectal tract (Fig. 713). In Birds the same relations are maintained ; here again a point-to-point representation of the retina has been physiologically demonstrated (Hamdi and Whitteridge, 1954). In addition to the main end-station in the tectum, however, a bundle of optic fibres in Birds has a thalamic termination in a basal optic ganglion (the ganglion ectomammillare of Edinger) (Fig. 714). Near the anterior border of the tectum a dorsal thalamic nucleus (the spiriform nucleus) receives fibres from this basal optic ganglion, in addition to fibres from the large spinal and bulbar tracts and descending fibres from the occipital area of the cortex and corpus striatum ; it has, however, no ascending projection, and the function of this thalamic system is therefore still entirely photostatic.

In the lower Vertebrates the superior colliculus which has evolved from the optic tectum receives the mass of optic fibres. In Mammals, however, the vast majority of the optic fibres (70 to 80%) terminates in the dorsal nucleus of the lateral geniculate body whence they are relayed by a cortical projection to the occipital cortex ; while, as in the lower Vertebrates, the minority goes either directly to the tectum (superior colliculus) in the brachium tecti or indirectly after being relayed in the ventral nucleus of the lateral geniculate body. In the colliculus a point-to-point representation from the retina has been reported in the cat, the goat, and the rabbit (Apter, 1945 ; Cooper *et al.*, 1953 ; Hamdi and Whitteridge, 1953). From this system there is, as always, no cortical projection. The ventral geniculate nucleus is thus phylogenetically the older and corresponds with the entire lateral geniculate body of the lower Vertebrates, decreasing in importance as the visual system swings from a tectal to a cortical orientation.

It is clear, therefore, that initially the visual system is developed in association with the postural and gravistatic systems in the tectum—the meeting-place of optic, static, tactile, gustatory and proprioceptive impulses, an area which, although it receives fibres from the cortex, sends no fibres to it. It is easy to underestimate the great importance of vision in orientation and equilibration, for in man these static functions are readily overshadowed by the apparent preponderance of the dynamic aspects of vision and the overwhelming importance of its sensory and cognitive functions. The phylogenetic importance of photostasis, however, is obvious. As evolution proceeds sensory functions assume greater and greater preponderance, and although the reflex and photostatic aspects of vision, which are as complex and elaborate in Primates as in the lower Vertebrates, are retained in the tectum, actually in the higher Vertebrates the epicritic visual functions

are transmitted through thalamic relay-stations in an ever-increasing degree to the cortex. This translation from a reflex to a highly integrative level allows the development of the central nervous system to proceed along two main lines—an advance from mass reflex reactions to more restricted but complicated patterns of behaviour, and an advance from a fixed rigidity to an extreme degree of plasticity and lability of response.

It follows from the late projection of vision to the cerebral cortex that ablation of this structure in the lower Vertebrates involves no visual incapacity. The fore-brain of Cyclostomes is completely, and of Fishes and Reptiles almost completely an olfactory brain and its removal has no visual effects, and, indeed, entails little alteration in the locomotion and the general behaviour of the animal (Magendie, 1824; Flourens, 1824). Fishes, it is true, lose the faculty of responding to unusual stimuli with initiative, become more purely reflex creatures than they already are, and are slower in their reactions (Janzen, 1933; Hosch, 1936; Meader, 1939; and others); while Amphibians lose spontaneity and initiative in their conduct and the conditioning of reflexes may fail (Diebschlag, 1934; Aronson and Noble, 1945). Nevertheless, a decerebrate frog will catch flies quickly and without difficulty (Schrader, 1887). It is not until Birds are reached that removal of the cerebral hemispheres induces a general listlessness and a marked lack of response; without a cortex the pigeon will maintain its bodily functions, will eat, mate and rear its young (Rogers, 1920-28), it will avoid obstacles and select its food visually, although some emotional responses can be elicited to visual stimuli (Schrader, 1888). Thus a decerebrate pigeon shows some impairment of the higher faculties of recognition and will not show the usual reactions to a threatening approach (Visser and Rademaker, 1935). Blindness can only be caused by destruction of the primary centres (Panizza, 1855; Schrader, 1887; Munk, 1890).

It is only in Mammals that the conduct of the animal is seriously disturbed by removal of its cerebral cortex, and even then it is only the Primates that are rendered blind by this mutilation; similarly it is only among Mammals that cortical stimulation involves motorial responses although the number of discrete movements that can be elicited in this way are few among the more primitive representatives of this class (less than 10 in Monotremes and Marsupials, v. Buddenbrock, 1937). In the lower Mammals there is a considerable equipotentiality of function in the cortex and, depending on the survival of incoming tracts, one part can readily act as substitute for another. Even if the entire cortex is removed, however, rabbits, after an initial period of blindness, can later differentiate between light and darkness (ten Cate, 1935) and decerebrate dogs will react and exhibit emotions to visual stimuli (Goltz, 1892; Pavlov, 1927). If, however, the occipital cortex alone is removed from Rodents (rabbit, rat), there is a loss of form vision only, while the faculties of perception of light and spatial localization are maintained so that the animal can move around,

avoid obstacles and recognize food by sight¹; these latter more fundamental aspects of vision, therefore, have subcortical integrations. In dogs the incapacity is greater; the animal retains the faculty of perception of light and can discriminate differences of intensity unimpaired, but in unfamiliar surroundings it gropes with its paws, moving cautiously as if blind (Goltz, 1892; Pavlov, 1927; Lashley, 1931; Marquis, 1934; Wing and Smith, 1942). Cats react similarly although they retain orientation and the discrimination of objects to a considerable extent in the dark (Smith, 1937). Monkeys suffer much more incapacity; light perception remains but discrimination between brightness is lost and performance is greatly impaired, particularly in bright light compared with conditions involving dark adaptation (Marquis and Hilgard, 1937; Kliiver, 1941). If part of the visual cortex of rats is removed, deficiencies in the response to visual conditioned reflexes are proportional to the amount removed irrespective of the area mutilated (Lashley, 1922-34), while in monkeys some responses which are lost can be relearned, presumably by a new area (Ades, 1946). Similar substitute areas can be utilized for auditory responses in dogs (Allen, 1945).

It is thus apparent that although a considerable degree of specificity of function appears for the first time in the neocortex of Mammals, it is still largely plastic with imprecise localization; only in man does ablation of the occipital cortex lead to permanent blindness with complete loss of all sensations of light. In him the only sub-cortical visual activity is pupillary, and in him alone is vision in its entirety a cortical function.

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¹ It is interesting that in amblyopia in squint, light perception and spatial orientation remain normal while form vision suffers.

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THE HORMONAL CONTROL

The control of the activities of organisms by chemical substances either derived from the external environment or elaborated in the internal environment is, of course, universal. In plant life we have already seen¹ that such chemical substances are the only means available for coordinating the activities of different parts and that many processes including flowering,

¹ pp. 10, 39.



FIG. 719.—ERNEST HENRY STARLING (1866-1927).

growth and phototropic bending are mediated by such substances, the most fully known among which are auxins. In the simplest unicellular animals the same mechanism of the diffusion of the chemical products of metabolism plays an essential role in the activities of the organism, and although in the higher animals greater reliance is increasingly placed on the more efficient and adaptable nervous mechanism, chemical coordinators are still retained, particularly to mediate those functions for which the controlling influence is required to last over considerable periods of time—growth and cellular differentiation, general metabolism, sexual activity, and so on. The spheres of influence of nervous and chemical control are by no means mutually exclusive for while a sudden response may be induced by the nervous mechanism, it is frequently maintained by the chemical, as is exemplified in the reaction of the sympathetic and the adrenals to situations of stress, or the complementary activities of nervous and chemical agencies in effecting changes in the chromatophores of Insects and teleostean Fishes. Chemical stimulators (or inhibitors) specifically elaborated to produce such effects are termed HORMONES.

The conception of hormones recalls the old theory of the humours which derived from the Aristotelian conception that all things were made up of the four common elements—earth, water, air and fire. The four humours which pervaded the body and determined its health—yellow bile (chole) from the gall-bladder, black bile (melancholy) from the spleen, blood (sanguine) from the liver, and pituita (or phlegm) from the brain. The conception of Vesalius that the phlegm secreted from the brain escaped by way of the infundibulum into the pituitary gland and thence was distributed throughout the body is very akin to the most modern conceptions of neuro-endocrine secretion that we are now to consider (Fig. 720).

The fact that organs deliver the products of their activity into the blood-current and thus influence bodily functions was known to Claude Bernard (1859) who introduced the term “internal secretions.” The word *hormone* (ὁρμάω, to rouse to activity), suggested by W. B. Hardy, was first applied to animal physiology by Starling (1905) with reference to the discovery of the manufacture of secretin by the pancreas (1902). The word was first applied to plant physiology by Fitting (1910) who found that a substance in the pollen of the orchid caused a swelling of the gynostemium of the flower. In botany the term *phytohormones* is often used, or, as the Russians have it, *florigens* (Cailahian, 1940). Since, in association with Sir William Maddox Bayliss, SIR ERNEST HENRY STARLING (1866–1927) was the discoverer of the first specific hormone and in view of his immense contributions to physiology in other fields, such as the nature of the body-fluids, the control of the intra-ocular pressure and a host of other equally revolutionary conceptions, I am introducing this section with his photograph (Fig. 719). My personal indebtedness to him as Professor of Physiology in University College, London, where he initiated me into the techniques of research, is indeed great.

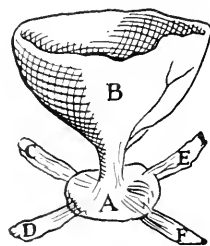


FIG. 720.—VESALIUS'S CONCEPTION OF THE FUNNEL (INFUNDIBULUM) (B) THROUGH WHICH THE PHLEGM TRICKLED INTO THE PITUITARY GLAND (A).

The four imaginary ducts C, D, E, F, carried the phlegm from the gland (Zuckerman).

It is obvious that to become effective to a multicellular organism, a hormone must be distributed through the circulation ; specialized endocrine organs are therefore found in Annelids, Molluscs, Arthropods and Chordates. It is not surprising that with a function akin to that of nervous tissue, these chemical messengers—or at any rate those which have been investigated—are initially in great part, both phylogenetically and embryologically, associated with the nervous system. Other origins, however, are common particularly in Vertebrates. In these, neuro-endocrine organs are found in the diencephalon—the hypothalamus, the pituitary and pineal glands—and in the medulla of the adrenal, a tissue of autonomic nervous origin which has migrated outside the central organization ; but in addition, from the endoderm there arise such hormones as the principles of the anterior lobe of the pituitary, thyroxin, and insulin, and from the mesoderm, the sex hormones and the steroids of the adrenal cortex.

Those hormones which mediate the migration of the retinal pigment are concerned with the sensory aspects of vision ; several others have associations with the action of light upon organisms and are therefore of interest from our immediate point of view ; to these we shall mainly confine ourselves, and since some of their reactions have already been discussed, a relatively short note is all that is called for at this stage. All of these concern the products of the neuro-endocrine system. We have already seen that certain cells of the central nervous system, particularly those of the cerebral ganglion in Invertebrates and of the diencephalon in Vertebrates, show a considerable degree of light-sensitivity¹ ; the dual function of the pineal body,² sometimes optical, sometimes endocrine, is an example of the same association. It is not surprising therefore that nerve cells in these regions should sometimes respond by the secretion of hormones to the direct stimulus of light and at other times to indirect stimulation through the eyes.

In general terms the neuro-endocrine system exercises a controlling influence over (a) the integumentary pigmentary system and the ocular pigments, (b) growth, differentiation and metamorphosis, (c) the development of the gonads and the regulation of the reproductive cycle, and (d) a number of processes in intermediate metabolism, principally affecting water, salts, oxygen and carbohydrates. A noteworthy feature of many of its activities is the rhythmic variation in several of these activities, either as a diurnal rhythm as is seen in the control of pigment migration and in some metabolic processes, or as cycles of longer duration such as are exemplified in moulting or the sexual rhythms.

NEURO-SECRETORY CELLS, that is, *nerve cells which also have the characteristics of glandular cells in that they show cytological evidence of secretory activity*,³ were first

¹ pp. 521, 525, 537.

² p. 711.

³ All these cells "secrete" active substances (e.g., acetylcholine) : this may be termed *neurohumoral activity*. *Neurosecretion* is a term best reserved for the activities of nerve cells which also possess the cytological attributes of glandular cells. For a complete discussion, see *Convegno sulla neurosecrezione*, *Pub. della Stazione Zoologica di Napoli*, **24**, Supp. (1954).

described by Dahlgren (1914) in the spinal cords of Fishes. They were later studied in the hypothalamus of Teleosts by E. Scharrer (1928) and in the eye-stalks of Crustaceans by Hanström (1931-34); but our present conceptions of the nature and function of neuro-endocrine complexes within the nervous system date essentially from the work of Berta and Ernst Scharrer (1937-45). It now seems obvious that the secretory activities of the central nervous system or of cells directly derived therefrom exert a considerable influence on the metabolism and activities of many

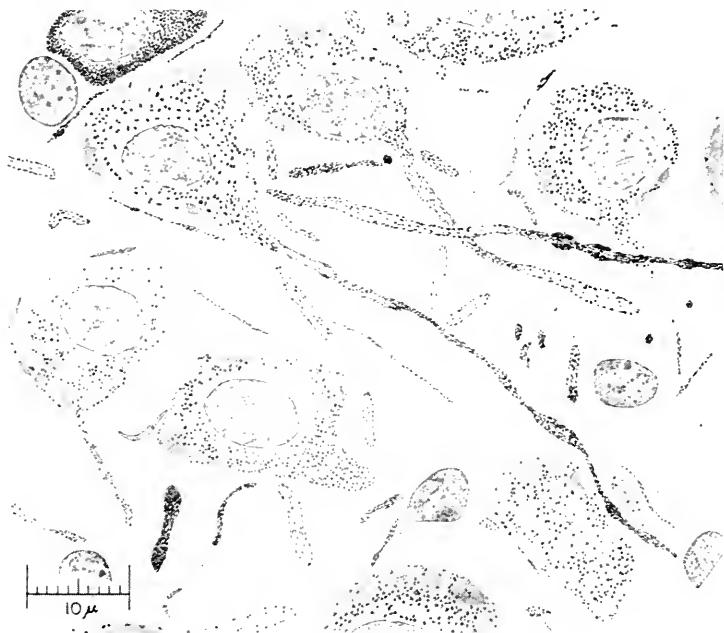


FIG. 721.—NEURO-SECRETORY CELL.

From the right nucleus paraventricularis of the rat. The granules of neuro-secretory material are seen in all the neurones and their axons. Note the characteristic fusiform enlargements in the axon emerging from the large cell in the upper left corner of the figure. The granule-laden segments seen everywhere are cut portions of the axons of other neurones at a distance from their cell bodies (Stuart W. Smith, *Amer. J. Anat.*, 89, 229).

species of animals including man. The secretions are elaborated within a large cell-body wherein they appear as granules and colloid-like material which are extruded along the axons, sometimes to be stored in organs in which the enlarged nerve-endings terminate (Fig. 721).¹ The latter are gland-like structures which serve as storage-release centres and, since it appears unlikely that the specialization for secretion has eliminated the capacity of these cells to act as conductors, a neuro-secretory cell can presumably trigger the release of its own accumulated secretion by conducting impulses to its endings at the storage-site. It follows that if it were formed from several completely independent groups of parent cells, such a "gland" might well serve as the storage-release centre for several hormones (see Brown, 1944-51; Brown, Sandeen and Webb, 1951; Brown and Hines, 1952; B. Scharrer, 1953; and others).

¹ The secretory products are most dramatically shown by staining with the chrome alum-haematoxylin-phloxine technique of Gomori (1941). See Bargmann (1949).

The occurrence of a neuro-endocrine system consisting of well-defined groups of neuro-secretory cells among Invertebrates is widespread. In its most primitive form it is seen in polyclad worms (Turner, 1946), but it becomes conspicuous in the more highly developed Annelids among which neuro-secretory centres are prominent, particularly in the cerebral ganglia where they inhibit maturation of the gametes (Bliss, 1951 ; Durehon, 1951 ; Bobin and Durehon, 1952). Neuro-secretory cells have also been described among Molluscs in the central nervous system of Opisthobranchs, Prosobranchs, Scaphopods and Cephalopods (Young, 1936 ; Gabe, 1949-53) ; the part played by simple hormones, probably of the nature of tyramine and betaine, in the regulation of the integumentary hormones of Cephalopods has already been discussed.¹ A similar neuro-secretory function is more common and effective in the nervous system of Arthropods ; indeed, in this phylum which does not possess a closed vascular system, no means is available for free circulation other than the rich hæmolymp supply which bathes the nervous system. In Crustaceans the neuro-endocrine system and its functions have received much attention ; it consists of an X-ORGAN and other groups of cells in the optic lobes and the cerebral and (probably) the first thoracic ganglia, while the storage-release organ is the sinus gland. In Insects the homologous system is the intercerebralis-cardiacum-allatum system. Among Myriapods, in the centipede there is an organ homologous to the X-ORGAN of Crustaceans (de Lerma, 1951) ; while among Arachnids, the chromatophorotropic principle of the nervous system can be correlated with similar neuro-secretory cells (Brown and Cunningham, 1941 ; B. Scharrer, 1941). In Xiphosurans the neuro-secretory system is large and is of peculiar ophthalmological interest in so far as the lateral rudimentary eye of the king-crab, *Limulus*, as well as the central nervous system, contains neuro-secretory cells (Scharrer, 1941 ; Waterman and Enami, 1954). Among the Proto-chordates, the neural gland of Ascidians secretes agents affecting pressor, melanophore and gonadotropic activities and is thus homologous with the pituitary gland of Vertebrates (Carlisle, 1951). And in the latter phylum the neuro-secretory system reaches its zenith in the hypothalamo-hypophyseal complex wherein the posterior lobe of the pituitary is linked with neighbouring hypothalamic nuclei. In Crustaceans, Insects and Vertebrates the neuro-endocrine system is of sufficient interest to merit special mention.

THE NEURO-ENDOCRINE SYSTEM OF CRUSTACEANS

Since the discovery of the small accumulation of neuro-secretory cells lying on the surface of the optic lobe in Crustaceans by Hanström (1931) and called by him the X-ORGAN, several other ganglia have been described in the eye stalks, the cerebral ganglion and possibly in the thoracic ganglionic mass which have comparable histological appearances and functions ; maps

¹ p. 93.

of these secretory areas are shown in Figs. 722 to 725, which also indicate the position of the SINUS GLAND, a gland-like structure also lying upon the eye-stalk which acts as a storage-release depot for the secretions of the neuro-endocrine cells (compare Fig. 692).

It is interesting from the historical point of view that the sinus gland was first considered to be the secretory organ of these hormones since most of the physiological

FIGS. 722 TO 725.—THE NEURO-ENDOCRINE SYSTEM OF CRUSTACEANS.

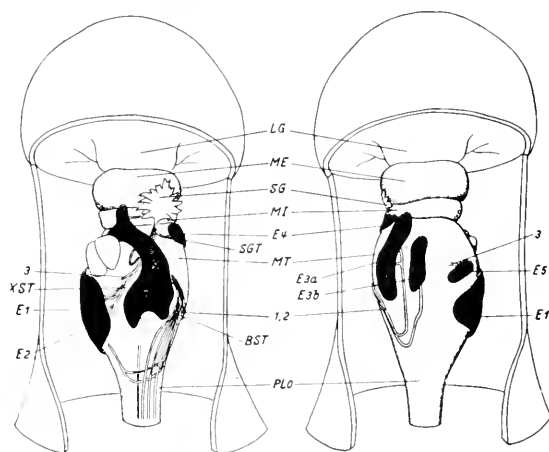


FIG. 722.

FIG. 723.

FIGS. 722 AND 723.—Neuro-secretory cells in the eye-stalk of a Crustacean.

Fig. 722 dorsal, and Fig. 723 ventral view of the right eye-stalk of *Cambarus*.

BST, nerve tract from the cerebral ganglion to the sinus gland; E1, the x-organ; E2-5, clusters of neuro-secretory cells; LG, lamina ganglionaris; ME, medulla externa; MI, medulla interna; MT, medulla terminalis; PLO, optic lobe peduncle; SG, sinus gland; SGT, tract of sinus gland; XST, nerve tract from the x-organ to the sinus gland; 1, 2, 3, fibre tracts (Bliss and Welsh).

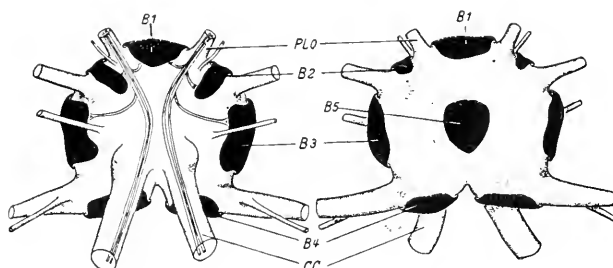


FIG. 724.

FIG. 725.

FIGS. 724 AND 725.—Neuro-secretory cells in the cerebral ganglion of a Crustacean.

Fig. 724 dorsal, and Fig. 725 ventral view of the cerebral ganglion of *Cambarus*.

B1-5, regions of neuro-secretory cells; CC, circum-oesophageal connective; PLO, optic lobe peduncle (Bliss and Welsh).

results attributable to the activities of the endocrine system were initially demonstrated by experiments involving the implantation or excision of this gland (Perkins, 1928 ; Perkins and Snook, 1932 ; Hanström, 1933-40 ; Welsh, 1941 ; Kleinholz, 1942 ; Brown, 1940-48). Later experiments on several species, however, showed that although these effects were frequently dramatic if the entire eye-stalk were removed, they were merely partial or temporary if this gland alone were carefully excised (Kleinholz, 1948-49 ; Havel and Kleinholz, 1951 ; Travis, 1951 ; Welsh, 1951 ; Passano, 1951-52 ; Bliss, 1951-53). Subsequent histological investigation with the appropriate technique demonstrated that this structure represented a gland-like accumulation of enlarged nerve-endings associated with the axons of neuro-secretory cells located in the x-organ and elsewhere in the eye-stalks and cerebral ganglion, indicating that the real role of the sinus gland is a storage-release centre of the colloid-like secretion of the cells of the neuro-secretory system (Bliss and Welsh, 1952 ; Carlisle, 1953 ; Bliss *et al.*, 1954).

The functions of the hormones secreted by the neuro-endocrine system of Crustaceans are complex ; those of greatest interest to us concern the integumentary and retinal pigmentation. In most cases there is no precise knowledge of the nature of these hormones or the site of their elaboration within the many ganglionic masses comprising the system. The *integumentary chromatophores* are regulated by three or four different CHROMATOPHOROTROPINS, some of which determine the concentration of pigment, others its dispersal. These have already been discussed¹ but it may be useful to recapitulate here that the release of these hormones is regulated by the degree of illumination and the nature of the background ; the receptor organs are the retinae, differential stimulation of the dorsal or ventral areas of which may determine the release of different hormones so that adaptation to the background is attained.

In addition to these environmental variations, we have already seen² that in many species a diurnal rhythmic release of the hormones causes a dispersal of pigment by day and its concentration by night, a habit which tends to persist in spite of artificial disturbances of the natural day-night sequence ; this rhythmic behaviour is an acquirement of the neuro-secretory centres (Koller, 1925-30 ; Perkins, 1928 ; Brown, 1940-46 ; and others).

Retinal pigmentation is under the control of at least two chromatophorotropins of an unknown chemical nature different from those responsible for changes in the colour of the integument, one regulating pigment migration in the dark, the other in the light. Here again, illumination and background are the determining factors in the release of the hormones and the effect is abolished if the optic nerve is cut (Smith, 1948 ; Sandeen and Brown, 1951-52) ; the hormone regulating pigmentary migration in the dark is often liberated in a persistent diurnal rhythm which gives a basic 24-hour variation to this activity also³ (Welsh, 1939-41 ; Brown, 1951 ; Brown *et al.*, 1951). In the prawn, *Leander*, it appears that migration of the distal retinal pigment depends on the hormones of the sinus gland modified by illumination,

¹ p. 93.² p. 19.³ p. 19.

while the proximal retinal pigment is independent of it (Knowles, 1949-50). So far as the migration of the former is concerned, the most likely hypothesis is that pigmentary migration is determined primarily by a dark-adapting and a light-adapting hormone, the production of both being regulated by a nervous centre (in the prawn, *Palaemonetes*, Brown *et al.*, 1952-53).

Reproduction in Crustaceans is controlled by hormones differing totally in nature from the chromatophorotropins (Matsumoto, 1951; Stephens, 1952) and is of considerable ophthalmological interest since, as we have seen,¹ the sexual cycle is frequently influenced through the eyes by photoperiodism. In prawns (*Leander*—Panouse, 1943-46), crabs and crayfish (Brown and Jones, 1947-49), such a hormone inhibits ovarian maturation and oögenesis, while excision of the gland in crabs results in arrested feminization or increased testicular development (Demeusy and Veillet, 1952; Demeusy, 1953; Cornubert *et al.*, 1952-53; Veillet *et al.*, 1953; Cornubert and Demeusy, 1955).

The control of growth and moulting are similarly determined (Bliss, 1951; Havel and Kleinholz, 1951; Passano, 1951; Stephens, 1955; and others), and in association with the moulting cycle there is a hormonal *regulation of the metabolism* of calcium and phosphorus (Kuntz, 1951; Travis, 1951), sugar (Kleinholz, 1950; Scheer and Scheer, 1951) and the rate of oxygen consumption (Bliss, 1951; Frost *et al.*, 1951).

THE NEURO-ENDOCRINE SYSTEM OF INSECTS

The headquarters of the neuro-endocrine system of Insects is a cluster of neuro-secretory cells in the PARS INTERCEREBRALIS of the protocerebrum (Fig. 726); their occurrence, discovered first in Hymenoptera by Weyer (1935), has been confirmed in a large number of species,² and in addition similar groups of cells have been found not only in the cerebral but also in the frontal and the sub-oesophageal as well as in some abdominal ganglia (Day, 1940; B. Scharrer, 1941). In relation with these cells, situated on the dorsal aspect of the cerebral ganglion, are two paired gland-like organs, the CORPUS CARDIACUM and the CORPUS ALLATUM, both closely associated in most insects and in some macroscopically inseparable; the first is comprised of both nervous and glandular tissue, the second is without nervous components so that they are somewhat analogous to the posterior and anterior lobes of the pituitary body of Vertebrates (Hadorn, 1937; Scharrer and Hadorn, 1938; Vogt, 1942; Bodenstein, 1943-44; and others). These three components form one neuro-endocrine complex, the corpus cardiacum being linked directly with the cerebral centre by large nerve-trunks carrying neuro-secretory material (Pflugfelder, 1937; Hanström, 1940; Nesbitt, 1941; Thomsen, 1954).

The control of *integumentary coloration* by chromatophorotropins in

¹ p. 16.

² Hymenoptera (bees, wasps, ants)—E. and B. Scharrer (1937); Hemiptera (bugs)—Wigglesworth (1939-40); Lepidoptera (butterflies)—Day (1940); Coleoptera (beetles), Trichoptera (caddis-flies), Diptera (flies)—Day (1940), Vogt (1942), and others.

Insects is limited to a small number of species, and the mechanism whereby it is achieved is relatively unexplored. The evidence suggests, however, that the main source of the hormones is the cerebral ganglion since its extirpation inhibits colour adaptation and the injection of extracts redistributes the integumentary pigment (*Carausius*—Dupont-Raabe, 1949–51). The hormones appear to be distributed through the agency of the corpora cardiaca while the allata seem to be inactive in the process (B. Scharrer, 1952). In some species the eyes are the sole receptors of the stimulation and their occlusion or section of the optic tracts inhibits all responses (the stick insect, *Dixippus*—Atzler, 1930). The diurnal rhythm in the migration

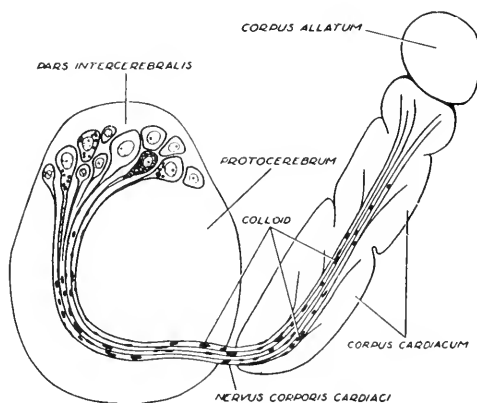


FIG. 726.—THE NEURO-SECRETORY SYSTEM OF AN INSECT.

A general diagrammatic representation (B. and E. Scharrer, 1944).

of the retinal pigment of some species suggests that here, also, an endocrine control may be active¹ (the noctuid moth, *Plusia gamma*—Kiesel, 1894 ; the beetle, *Bolitotherus cornutus*—Park and Keller, 1932).

The important *gonadotropic hormones* controlling reproductive processes and the development of the sex organs are elaborated mainly in the corpora allata which in some species may be under the control of the cerebral ganglion (Altmann, 1952 ; B. Scharrer, 1952), while the complicated processes of *growth, moulting and differentiation* with all their spectacular changes are integrated by hormones mainly elaborated in the prothoracic gland.² *Metabolic processes* such as oxygen consumption are effected through the pars intercerebralis and the corpora allata (Thomsen, 1949–52).

THE NEURO-ENDOCRINE SYSTEM OF VERTEBRATES

The neuro-endocrine mechanism of Vertebrates is centred in the extremely complex aggregation of nuclei and secretory organs known as the hypothalamo-hypophyseal system ; from the hormonal point of view the most interesting section in this part of the central nervous system is the

¹ p. 15

² Review see Wigglesworth, 1934–40 ; Bodenstein, 1942 ; B. Scharrer, 1953.

NEUROHYPOPHYSIS. Several of the hypothalamic nuclei are made up of typical neuro-secretory cells for which the posterior lobe of the pituitary body (pars nervosa) and the median eminence of the pituitary stalk serve as a storage-release organ (Fig. 727) (Scharrer and Scharrer, 1945 ; Weiss and Hiscoe, 1948 ; S. W. Smith, 1951 ; Zuckerman, 1954 ; van Dyke *et al.*, 1955 ; and others). The posterior lobe of the pituitary is thus homologous with the corpus cardiacum of Insects, the anterior (non-nervous) lobe with the corpus allatum. In Fishes the essential centres of this endocrine function are two paired nuclei—the nucleus pre-opticus and the nucleus lateralis

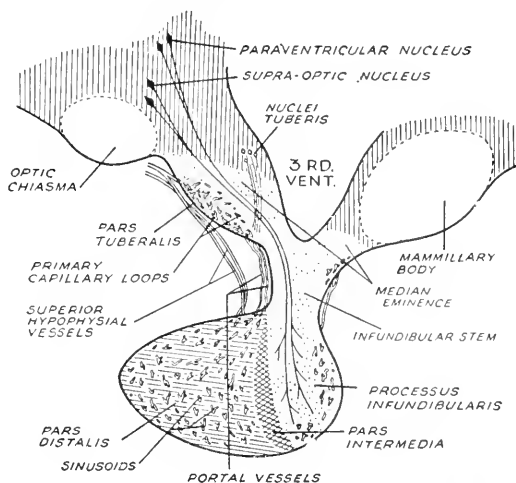


FIG. 727.—THE NEURO-ENDOCRINE SYSTEM OF A PRIMATE.

Diagram to indicate the relations of the pituitary gland to the hypothalamus (after Zuckerman).

tuberis (E. Scharrer, 1928 ; Palay, 1943–45) ; in Amphibia the nucleus pre-opticus alone (E. Scharrer, 1933 ; Gaupp and Scharrer, 1935) ; in Reptiles the two divisions of the nucleus pre-opticus are involved—the supra-optic and paraventricular nuclei (Gaupp and Scharrer, 1935) ; and in Mammals to these may possibly be added a third group of cells, the mammillo-infundibular nucleus¹ (S. W. Smith, 1951 ; Hanström, 1952–53 ; Zetler, 1953 ; and others) ; all of these are connected to the pars nervosa of the pituitary and the cells of the median eminence of the stalk by the hypothalamo-hypophyseal tract to form the neurohypophysis. The possibility of the existence of secretory cells in the posterior lobe of this composite organ, either in the pars nervosa or the pars intermedia, is a matter which

¹ These three nuclear masses, made up of large vacuolated cells with eccentric nuclei, form the anterior group of hypothalamic nuclei. The *supra-optic nucleus* lies close to the pituitary stalk immediately above the optic chiasma at the anterior end of the optic tract and projects a short distance along the anterior aspect of the tuber cinereum. The neighbouring *paraventricular nucleus* is a flat plate lying close against the ependymal lining of the third ventricle. The *mammillo-infundibular nucleus* is close to the cephalic end of the supra-optic nucleus.

requires further elucidation, as also does the mechanism, if any, whereby the hypothalamus may control the anterior lobe of the pituitary body (see Zuckerman, 1954).

The activities of the neuro-endocrine system in Vertebrates as centred in the hypothalamo-hypophyseal complex are extraordinarily extensive and varied, for the hypothalamic nuclei exercise a supervisory control over most of the other endocrine organs. They take direct control of the pituitary body itself with its immense influence on the processes of pigmentation, growth, diuresis and intermediary metabolism and its vasopressor and oxytocic effects; in addition, they exercise a quick-working stimulation of the adrenal medulla through the sympathetic, and through the medium of the pituitary they exert a slow-working control over a host of endocrine activities, stimulating the thyroid by means of the thyrotropic hormone, the steroids of the adrenal cortex through adrenocorticotrophic hormones, as well as controlling the development of the sex organs and the reproductive rhythms through the gonadotropic hormones. The holistic nature of endocrine balance is seen in the feed-back from these peripheral organs to the hypothalamus by hormones of opposing nature which inhibit the excessive production of those stimulatory agents by the neuro-endocrine system. Most of these activities do not affect the eye; but some do.

The role of hormonal control over the *integumentary pigment* of Fishes, Amphibians and Reptiles has already been discussed at length.¹ It will be remembered that environmental changes in many species are effected solely by the control of mutually antagonistic hormones associated with the pituitary, the release of which is determined by stimuli operating through the eyes (Cyclostomes, Selachians, Amphibians² and some Reptiles); in other species a nervous control is partially (Teleosts) or entirely (chameleon) responsible. Similarly, the cyclic diurnal variation of the coloration which occurs in many of these types—Cyclostomes such as the lamprey, Amphibians such as salamander larvæ and frogs, and Reptiles such as the lizard, *Anolis*, the chameleon and the American horned "toad," *Phrynosoma*—is due to the rhythmic release of the appropriate hormones by the pituitary under the control of its associated hypothalamic centres. Hypophysectomy abolishes the darkening and lightening of the skin of the frog (Hogben, 1924), and in the lizard, *Anolis*, suppresses the rhythmic change from brown during the night to green during the day (Rahn and Rosendale, 1941).

In a similar manner there is evidence that the pigmentation of the iris in the frog is influenced by the hypophysis (del Castillo, 1955).

The migration of the *retinal pigment* of Vertebrates³ is essentially a direct response to light and, unlike that of Crustaceans, shows little indication of hormonal control.

¹ p. 96.

² After removal of the eyes from the toad, *Bufo*, some of the responses of the melanophores to illuminating backgrounds persist, perhaps due to the direct action of light on the hypothalamus (p. 96).

³ p. 61.

Some evidence, however, has been made available in the frog. Derman (1949) found that while hypophysectomy had no effect on the retraction of the retinal pigment during dark-adaptation, it slowed but did not inhibit the migration of pigment during light adaptation, while injection of an extract of the intermediate lobe of the pituitary body provoked the migration characteristic of light-adaptation in the dark-adapted hypophysectomized frog. This action was abolished after section of the optic nerve. Damage to the hypothalamus has also been said to influence the migration of the retinal pigment in this animal (Kitashoji, 1953 ; Nakamura, 1954), an effect also shared by epinephrine (Nakamura, 1955) and Pregnenolone, a relation of the adrenal corticosteroids (Pannarale, 1952). It is clear, however, that nervous influences predominate over any effect that may be exercised by the pituitary-hypothalamic system in Amphibians.

In the higher Vertebrates any such effect is even more insignificant. It may, however, be of interest that Rubino and Pereyra (1948-50) have claimed that the degree of light-sensitivity in man undergoes a diurnal rhythm, being increased during the night ; the fact that this faculty is maintained unimpaired in the amblyopic eye or in patients affected by primary pigmentary degeneration suggests that this cyclic change is centrally determined. There is, indeed a considerable body of opinion which maintains that this latter disease may sometimes be associated primarily with a hypothalamic-endocrine disturbance, the most dramatic instance of which is seen in the Laurence-Moon-Biedl syndrome (see Zondek and Koehler, 1932 ; Zondek and Wolfsohn, 1940 ; Alajmo and Rubino, 1952).

The *gonadotropic action* of the hormones elaborated in the anterior lobe of the pituitary in Vertebrates is well established,¹ both in determining the development of the organs of sex and governing the cyclic activities of reproduction. The rate and rhythmic variation of the secretion of the gonadotropic hormone in Mammals are regulated by the tuber nuclei of the hypothalamus, isolated injuries to which have caused sexual disturbances in all Mammals so far studied² ; delicacy of adjustment and integration is thus achieved and in the absence of this nervous control the secretion continues without coordinated balance. In many Vertebrates the sexual rhythm is adapted to the most favourable season of the annular solar cycle and one of the most potent influences in determining this process is light. We have already seen³ that the sexual maturation of many Fishes, Reptiles, Birds and Mammals is determined in this way by photoperiodism, and that the process can be accelerated or retarded by altering the relative duration of light and darkness in the diurnal cycle. In most cases the stimulus is retinal in origin and neural in conduction along the optic nerve and is relayed not to the visual centres of the brain but to the hypothalamus which activates the pituitary (Le Gros Clark *et al.*, 1937-39) ; and blinding, hypophysectomy or section of the nervous connections between the hypothalamus and the pituitary destroys the cycle, while the injection of pituitary extract activates it (Hill and Parkes, 1933 ; Thomson, 1951-54 ; Thomson and Zuckerman, 1953-54 ; Donovan and Harris, 1956). In some

¹ For reviews, see Allen (1939), Burrows (1949), Brown (1950), Galgano and Mazzi (1951).

² Guinea-pig, rabbit, ferret—Brooks (1938-40), Bard (1940), and others.

³ p. 16.

Birds, on the other hand, and perhaps in some Mammals, light appears to activate the pituitary or the central nervous system directly, perhaps through the spectral sensitivity of a coproporphyrin (Parker *et al.*, 1952).¹ In ducks, for example, Benoit and his collaborators (1952-54) have shown that light, concentrated as it traverses the eye, travels through the orbit and reaches the hypothalamus, thus regulating the gonadotropic action of the hypophysis; excision of both eyes does not inhibit but, by increasing transmissibility, rather enhances the gonadotropic activity, and the pituitary body of immature ducks stimulated by increased illumination can excite oestrus when implanted into immature mice.

The seasonal migrations associated with the sexual cycle of Birds and Mammals is similarly controlled by photoperiod,² as well as the seasonal moults and changes of colour in the feathers or hair of many Birds or Mammals.³ In these cyclic changes the pituitary is the most potent factor (Witschi, 1935; Brown and Rollo, 1940; Leshner and Kendeigh, 1941; Kobayashi and Okubo, 1955); similarly, hypophysectomy abolishes the cyclic moulting of ferrets (Bissonnette, 1935-38). It would seem, indeed, that the pituitary is the only endocrine organ involved in these activities in Mammals since castration or thyroidectomy has no such effect on the varying hare (Lyman, 1943).

The influence of the hypothalamo-hypophyseal system on the *growth, metamorphosis and metabolism* of Vertebrates and its pressor effects on the circulation are potent but are without marked interest in our survey of the development of the visual system. An associated optic-diencephalic relationship, however, may be seen in the observation that in the rabbit exposure to light increases the urinary excretion of 17-ketosteroids (Siliato, 1955). Another exception may be constituted by the *photoglycaemic reflex* recently explored by Italian workers but not otherwise investigated. It was originally claimed by Cavallacci (1937) that stimulation of the retina by light altered the metabolism of sugar, the blood-sugar curve being normally different if the sugar were ingested by day or by night. This finding has been confirmed by Bassi (1945) and Rubino and his collaborators (1948) who concluded that abnormalities occurred in persons affected by glaucoma and primary pigmentary degeneration of the retina, both of which diseases may have hypothalamic implications. In this connection the suggestion that dark-adaptation is impaired in adiposo-genital dystrophy, a disease associated with hypothalamic disturbances, may possibly be of interest (Landau and Bromberg, 1955).

A relationship, still vague but yet undoubted, exists between the *intra-ocular pressure* and the endocrine system, particularly the hypothalamo-hypophyseal complex, and claims have been put forward from time to time that primary glaucoma is often an expression of a diencephalic disturbance (Hess, 1945; Zondek and Wolfsohn, 1947; Magitot, 1947; Alajmo and Rubino, 1952; and many others). The pupillary changes described by Lowenstein and Schoenberg (1944) point to some neurogenic sympathetic disturbance in this region of the brain in this disease. That a hypothalamic centre exercises some control over the intra-ocular pressure is clear (v.

¹ Ivanova (1935) produced evidence that the skin may also be a possible receptor in the house sparrow, *Passer domesticus*.

² p. 19.

³ p. 21.

Sallmann and Lowenstein, 1955; Gloster and Greaves, 1957), an influence which is probably responsible for the cyclic diurnal variations in the normal intra-ocular pressure and, in part perhaps, for the exaggeration of those variations that characterize primary glaucoma (see Duke-Elder, 1952-7); but whether its action is mediated by nervous or hormonal factors or both is still unknown. Hyperpituitarism has been most commonly associated with ocular hypotony (Imre, 1921; Marx, 1923), while the reputed cyclic variation of the ocular tension with the menstrual cycle or in association with pregnancy, falling in the progestational phase of both and rising in the oestrogenic post-menstrual period or after delivery, is suggestive (Salvati, 1923; Marx, 1923; Becker and Friedenwald, 1953), as also is the reported reduction of tension in glaucomatous patients by progesterone (Obal, 1950; Posthumus, 1952; Becker and Friedenwald, 1953; and others). The most positive assertion has been made by Schmerl and Steinberg (1948) and Schmerl (1955) who claimed that the spinal fluid of rabbits contained two active principles, presumably secreted by the posterior lobe of the pituitary body into the third ventricle, one, acting on parasympathetic centres ("hyperpiesine"), raising, the other, acting on sympathetic centres ("miopiesine"), lowering the intra-ocular pressure. In the rabbit (a nocturnal animal) the intra-ocular pressure is said to increase during light and to fall during darkness because of this mechanism; in man (a diurnal animal) the reverse occurs. More experimental investigation, however, is required to substantiate these claims which are still somewhat nebulous and are not yet based on unequivocal evidence. As in other spheres of physiology and pathology, our knowledge of the complex and far-reaching influence of the diencephalic-hypophyseal system upon the vegetative physiology of the eye is still in an elementary stage.

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PART III

THE FUNCTION OF THE EYES OF ANIMALS

THE VISION OF INVERTEBRATES

THE VISION OF VERTEBRATES



FIG. 728.—KARL VON FRISCH (1886——).

CHAPTER XVII

THE VISION OF INVERTEBRATES

I am introducing this chapter on the function of the eyes of Invertebrates with the photograph of KARL VON FRISCH (1886 —) (Fig. 728), who has devoted his long and fruitful life to the fascinating study of animal behaviour—and still continues to do so. Born in Vienna, he studied in Munich and successively became Professor and Director of the Zoological Institutes at the Universities of Rostok (1921), Breslau (1923), Munich (1925), Graz (1946), and again Munich (1950) where, as this book is being written, he is still pursuing his close and intimate study of the habits of insects. Taken as a whole, his life as a biologist, spent observing the behaviour of his experimental friends in the water and in the countryside, must have been a delightful one ; he obviously enjoyed it and no one can read his published works without realizing that fact can indeed be more exciting and of more interest than fiction. The greater part of the first years of his studies was devoted to the vision, and particularly the colour vision, of fishes, a subject in which, as we shall see in the following chapter, he became a great authority, opposing the views of Carl von Hess (Fig. 735) and eventually winning the battle. The latter part of his life has been largely spent observing the habits of bees. Much of the fruits of this we have already studied in the chapter on the influence of light on movement.¹ There are few romances in science more pleasant than the convincing and far-reaching results he has obtained in the study of the extraordinarily complex behaviour of these insects in the meadows of Central Europe ; and there are few pieces of biological work carried through with greater perseverance, with greater thoroughness and to greater purpose.

METHODS OF INVESTIGATION

The scientific estimation of the visual capacity of animals is notoriously difficult. It is a difficult problem even in man for sensations are individualistic and subjective and the language of introspection is usually unsafe ; in the lower animals the difficulties become infinitely greater for the only criterion whereon we can pass judgment is the observation of their reactions to various stimuli ; we have no knowledge of how far their experiences coincide with our own, and no right to equate the two.²

From the scientific point of view the observation of animal behaviour in ordinary uncontrolled circumstances can provide much useful information regarding their sensory experiences, but from such evidence our conclusions can only be drawn with reserve. This approach is full of pitfalls even in human subjects. A red-green colour-blind person will say that he can appreciate red and green and usually behaves as if he does so ; and we have little idea of what

indeed he does see. For this reason König gave up the method of introspection entirely and trusted only to colour-matches in his investigation of colour-blindness ; only if every colour in the spectrum could be matched by a mixture of a given pair of colours should the subject be considered a dichromatic colour-blind. There are occasions, however, when the observation of the behaviour of animals in their natural surroundings can yield satisfying results. We have already noted many instances of such oecological research, for example, in the study of the conduct of different Arthropods in their orientation towards light ; a particularly good example is von Frisch's experiments on bees, or the means of orientation employed by birds in navigation. These methods, however, valuable as they are, are applicable only to certain restricted types of complex behaviour of a nature such that other incidental variables can be neglected.

Two more generally applicable methods of research are available. In the *objective methods* of approach a measurable physical phenomenon presumably determined by a specific stimulus is observed—a contraction of the pupil to light, for instance, or an electroretinographic response—and it is assumed that this reaction bears a relatively constant relation to events on the sensory level. If a response of this nature follows stimulation by one band of wave-lengths of light and not by another, for example, it is probable that the first gives rise to a sensation and the second does not. A further analysis is possible by the study of reflex responses. If an animal exhibits characteristic reflex reactions to varying stimuli it is reasonable to suppose that these affect it in different and specific ways. The optomotor reaction illustrates this. If an animal, be it insect or vertebrate, is faced with a revolving striped drum and reacts to the succession of stimuli thus presented to it by compensatory movements of its eyes or its body, we can assume that the alternating stimuli have a different effectivity ; or if an animal salivates when presented with one stimulus associated by training with food and not with another, the deduction seems inescapable that a discrimination is made between the two stimuli ; but whether the differentiation remains on the reflex level or is appreciated as a sensation is sometimes problematical.

The elicitation of such reflex responses, however, although suggestive, gives us little idea of the conscious appreciation of sensations and their effectiveness in determining conduct. A more satisfying approach is the *subjective method* of the study of what appears to be conscious behaviour. The simplest technique in this respect is a study of " preference " : if an animal goes towards light and avoids darkness, or vice versa, it evidently can distinguish between them ; a similar argument applies to a fish which swims towards a red rather than a green light. How far this conduct implies that the discrimination is

based on different sensory experiences is, however, doubtful. It has been generally accepted in the case of the worm which emerges in twilight and hides again in daylight ; but does it equally apply to the protozoan which shows the same response ? We do not know the answer to this riddle.¹

A more analytical method is the application of *training techniques* which, incidentally, are more susceptible to scientific control. Thereby an animal is trained to respond to or reject one stimulus to the exclusion of all others by an appropriate reward or punishment, the stimulus

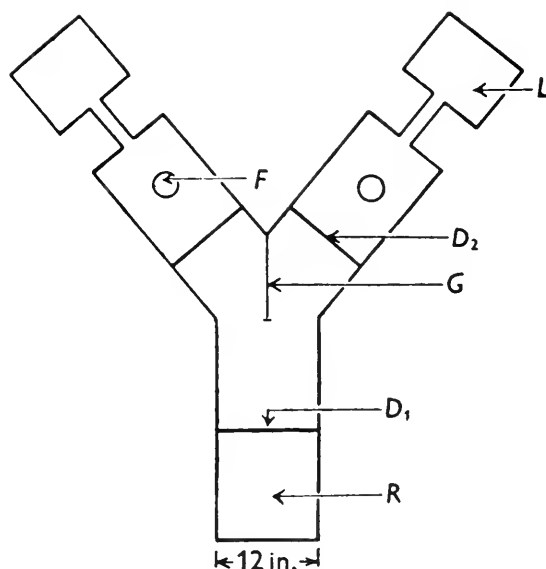


FIG. 729.—GROUND PLAN FOR DISCRIMINATION BOX.

L, light box. *F*, food ; *D*₁, hinged door ; *D*₂, hinged door with 3 × 3 in. opal glass panel ; *G*, glass partition ; *R*, restraining chamber. The box is 13 in. high (R. Gunter, *J. Physiol.*, 1951).

being more minutely differentiated from related stimuli as the process of training proceeds. The disadvantage of the method is the limitations of its applicability since it requires more intelligence, consistency in behaviour and amenability than most animals possess ; moreover, an experiment of this type must excite the animal's interest so that the technique would be expected to break down if the sensation in question were not of importance in its life.

A simple and typical experimental set-up for such a training experiment is seen in Fig. 729. In its essentials it is a Y-shaped "discrimination box" or maze wherein the animal is first retained in an outer chamber and then, entering

¹ p. 102.

the main chamber, is offered the choice of two stimuli ; these, for example, may be light stimuli made up of two illuminated milk-glass panels set into hinged doors and lit from behind so that they can be suitably varied in intensity, hue or saturation. Either of these the animal can open to receive a reward (food) or punishment (an electric shock). Trained initially to go towards one (the positive) of two well-differentiated alternative stimuli and to avoid the other, the negative stimulus is approximated progressively to the first until the limit of discrimination is reached. Throughout the experiment the relative positions (right or left) of the two stimuli are randomly alternated, while other stimuli (olfactory, etc.) are eliminated as by placing similar food in each box, that in the negative box being inaccessible. Such training techniques, of course, are laborious, several hundred "runs" being usually required in each experiment ; moreover, they are time-consuming for much cannot be accomplished at one session lest fatigue be induced or interest lost ; and they are restricted to species which are relatively intelligent and docile, for a stupid or an untrainable animal or one that gets cross or sulks is useless.

It is also to be remembered that any response of this nature made by an animal depends upon complex factors ; few stimuli are in fact simple, most involve more than one receptor, and all responses are complicated by mutual excitations and inhibitions. For the animal reacts not to one stimulus alone (such as food) but to a complex situation wherein each stimulus must be differentiated against a changing background and varies with past experience and its present psychological state. Even in the most adequately controlled experiments in the laboratory an ideal environment can rarely be realized. The very fact of the artificial isolation of the stimulus is outside the animal's natural experience and thereby something important in the experiment is lost. It follows that the results of such analyses can be accepted only with reservation ; indeed, any claim that a scientifically exact appreciation of the physiology or psychology of any animal can be based on conditioning experiments is illusory.

Within these limits, the method undoubtedly produces results in terms of sensational responses of greater reliability than any other and forms the best means of analysing the nature of the sensation concerned. Considering these difficulties, however, as well as the variation in psychology between different members of the same species and the probable differences in apperception and interpretation between any species and our own, it is not surprising that the results thus obtained have often been inconsistent.

THE LOWER INVERTEBRATES

PROTOZOA. We have already seen that Protozoa exhibit fixed reactions to a variety of "sensory" stimuli—light, heat, gravity, contact, electrical shock—the only observable response being a tropism. We have also seen that there is no observable difference in behaviour

in respect to these different modalities but that, on the other hand, they may be additive in their effect. Whether the reaction is positive or negative there is no evidence that the response is associated with subjective awareness ; and although a temporary process of conditioning may exist due to the cumulative effects of previous stimuli,¹ there is little evidence of any true capacity for learning. Soest (1937), for example, claimed that an association with electric shocks could condition an avoidance of light in *Paramœcium*, but this behaviour may well have been determined by the accumulation of metabolites (Dembowski, 1950). It would therefore seem that apart from responses which are explicable on a purely physico-chemical basis, we have no knowledge of "vision" in the sense of perceptual awareness in this phylum (see Wichterman, 1953).

CŒLENTERATA. Among Cœlenterates there is more evidence for assuming the existence of a lowly organization of some aspects of conduct on a reflex level as well as the presence of associated memory. The spontaneous movements exhibited by several species either of swimming or "stepping" whether the environment is changed or remains constant, are obviously the result of controlled activation and inhibition² ; the same type of conduct is seen in the daily rhythms in the activity of sea-anemones and jelly-fish, such as those determined by tidal changes, which may persist for some considerable time after the stimulus has been artificially removed.³ That purposive reactions with memory associations also exist is suggested by such types of behaviour as the assumption by the anemone, *Actinia*, of the same position in an artificial aquarium as it occupied in its natural rock (van der Ghinst, 1906 ; Bohn, 1908), the apparent intelligence of the anemone, *Antholoba*, in climbing on the back of a crab (Brunelli, 1910), or the rejection of unsuitable food after several trials by such anemones as *Actinia*, *Tealia* and *Cribrina* (Fleure and Walton, 1907 ; Gee, 1913 ; and others). In spite of these activities, however, so far as we know, the phototactic reactions of this group are completely automatic and fixed, and indeed have been found to remain unchanged after two generations have been exposed to abnormal lighting conditions (Ewer, 1947).

ECHINODERMATA. In this phylum, again, although some training ability in the starfish, *Asterias*, is suggested by the observations of Jennings (1907) on its capacity to right itself, or of Ven (1921) on its ability to escape from a confined position, there is no proof of any visual reaction except a rigid and unvaried phototactic response without detectable evidence of subjective appreciation.



Paramœcium



Sea-anemone



Jellyfish



Starfish

¹ p. 36.

² Haug (1933) in *Hydra* ; Batham and Pantin (1950) in the sea-anemone, *Metridium*.

³ Piéron (1909) in sea-anemones ; Horstmann (1934) in the jellyfish, *Aurelia*.

THE VISION OF WORMS

As would be expected from the extreme primitiveness of their ocular structures, the vision of worms is limited to an appreciation of the presence or intensity of light associated with a light-shadow reflex usually of a photo-negative type ; as we have seen, in some species a directional localization may be possible. In the UNSEGMENTED WORMS the simple photo-negative reaction is the only response. Planarians, for example, are always found in dark places beneath stones or the leaves of water plants, vigorously retreating from light whenever they are exposed to it (Taliaferro, 1920). Some such response to light still remains when the eyes have been removed, the animal depending on light-sensitive cells scattered over the surface of the body. There is evidence, however, for the first time in the animal kingdom, that the rigid phototactic response can be modified in a very crude manner by training. The Polyclad, *Leptoplana*, for example, is quiescent in the dark and moves when illuminated, but contact of the head-end with a solid object stops the forward movement. Hovey (1929) found that by simultaneously illuminating the worm and touching it so as to prevent it from creeping forward, the photo-kinetic reaction was completely inhibited ; a similar conditioning process to electric shocks was demonstrated in *Planaria gonocephala* by Dilk (1937). After removal of the cerebral ganglion these modifications of the simple phototactic response cannot be elicited, so that this structure is necessary for the development of this elementary learning process. In assessing the importance of these reactions to light in the life of the animal, however, it must be remembered that the general behaviour of unsegmented worms is determined not so much by their light-sense as by the more fully developed chemical sense and the sense of touch which responds with great sensitiveness to the slightest movement of the water in which they live or to objects with which they come in contact.

More work has been done on the light-sense of SEGMENTED WORMS, particularly upon the earthworm, *Lumbricus*.¹ It will be remembered² that in this animal the light-sensitive cells are concentrated mainly at the two extremities. In very dim illumination (less than 0.00118 m.c., W. N. Hess, 1924) the animal is photo-positive, and in ordinary daylight illumination, photo-negative—it must avoid light since, in fact, exposure to strong sunlight for one hour may cause paralysis, for several hours, death. It follows that on emerging from its burrow at any time except at night or in the dim twilight of morning or



Planarian

*Leptoplana**Lumbricus*

¹ Hoffmeister (1845), R. Hesse (1896), W. N. Hess (1924), v. Buddenbrock (1930), Seg. (1933), Unteutsch (1937-38).
² 190.

evening, either end will at once retract into the safety of its retreat. Its more complex reactions to light when travelling on the ground have already been described.¹ A similarly high degree of sensitivity is seen among certain polychæte worms, particularly the tubiculous types. In these the light-and-shadow reflex is very marked; so sensitive are they to light that Andrews (1891) found that if a hand were moved in the air at a distance of a metre from the water containing the animals, they withdrew themselves into their tubes as soon as the shadow fell upon them.

In segmented worms, however, the potentialities of habituation and learning have evolved to a considerably greater extent; that earthworms, indeed, have a modicum of intelligence was known to Darwin (1881) who noted the deft way in which by trial-and-error, profiting by previous experience, they transported leaves of various types to their burrow or collected little stones to guard its entrance.² Again, *Hydroides*, if collected from shallow water, reacts promptly to shadows in the aquarium, but individuals collected from deep water remain inactive presumably from lack of experience in a shadowless environment; a like passivity is rapidly assumed by reactive specimens from shallow water if they are isolated from shadows for some time in the laboratory (A. W. Yerkes, 1906; Hargitt, 1906-9). Similar habituations to light-and-shadow stimuli have been found also in polychæte worms (Bohn, 1902) and leeches (Gee, 1913). Moreover, in these species the normal response can be varied by conditioning. Thus the polychæte, *Nereis*, if presented with food together with a sudden increase or decrease in illumination, can be trained after only six trials to respond to the change in illumination alone whether it is positive or negative (Copeland, 1930), while by a similar association with tasty food or other stimuli a reversal of the usual reaction to light can be induced in a number of worms such as *Hydroides* (A. W. Yerkes, 1906), *Nereis* (Copeland and Brown, 1934), *Lumbriculus* (Raabe, 1939) and *Lumbricus* (Wherry and Sanders, 1941). Finally, several Oligochaetes and Polychætes have shown a considerable ability to learn the correct turning in a simple T- or Y-maze; propelled forwards by illumination of the hind region, rewarded by a warm dark cell or punished by an electric shock or an unpalatable salt solution, they can after many trials (up to 200) be taught to turn in the required direction, a capacity unimpaired by excision of the supra-œsophageal ganglion.³

In worms, therefore, in which a ganglionated nervous system first appears, for the first time in evolution the response to light has been shown



Nereis

¹ p. 53.

² See also Málek, 1927.

³ In Oligochaetes: *Allolobophora* (R. M. Yerkes, 1912), *Eisenia* and *Lumbricus* (Heck, 1920), *Heliodrilus* (Swartz, 1929); in the polychæte, *Nereis* (Copeland, 1930; Fischel, 1933; Copeland and Brown, 1934).

to become something that is not rigid and entirely automatic ; it can be modified by experience and training, while vision, although still a secondary sense, apparently becomes endowed with some degree of awareness and meaning.

THE VISION OF MOLLUSCS

From the functional point of view in most Molluscs vision is secondary to the olfactory or tactile sense ; this would be expected in view of the primitive structure of the eyes of most types for, with the exception of Cephalopods, they are rarely capable of detailed visual resolution. It has been contended that land Molluscs (snails, slugs, etc.) which seldom emerge except in twilight and retract their eyes within their tentacles on exposure to bright light, are blind (Yung, 1913) (Fig. 188). A directional appreciation of light is possible, however, and quick movements can be readily detected (Föh, 1932 ; Grindley, 1937) ; but there is no evidence of the appreciation of colour (Mundhenke, 1955). These animals, however, are highly myopic and experiment has shown that objects can rarely be appreciated more than a few centimetres away, although farther in subdued than in bright light (Willem, 1892). Vision does not thus appear to dominate behaviour. On the other hand, Gastropods are extremely sensitive to the slightest movement of the air or any jarring of the surface on which they crawl, while their sense of smell is so acute as to dominate most of their behaviour : food, for example, is sought almost by scent alone.

In littoral lamellibranch Molluscs it would seem probable that vision is generally limited to the appreciation of light and shadow, but this appreciation may be unusually acute. Whether the ocelli are situated on the siphon or the mantle-edge the slightest shadow often induces a response. Thus Patten (1886) found that in the Noah's-ark shell, *Arca*, the mantle contracted and the valves closed quickly if the faint shadow of a hand or a pencil fell upon them. It is interesting that sensitivity does not always vary with the elaboration of the structure of the eye, for the same observer found that an even more sensitive response was given by *Avicula* which is provided with only a few ill-developed ocelli; even the eyeless mussel, *Anodonta*, reacts to a passing shadow owing to its dermal sensitivity to light (Braun and Faust, 1954).¹ The rapidity with which oysters close their shells on the passing of the shadow of a man or a boat is well known. A similar sensitivity to passing shadows characterizes the ocelli in the siphons of littoral Lamellibranchs (Hecht, 1919 ; Koller and v. Studnitz, 1934, in *Mya*) ; and it is obvious that such types which live between the tide-marks and protrude their siphons and occasionally



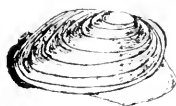
Snail



Slug



Avicula



Anodonta



Mya

¹ p. 114.

portions of their shells outside their burrow, will depend much for their survival on their ability to withdraw into safety before the arrival of their many enemies. *Pecten*, with its elaborate eyes, is an exception, perhaps because this animal may use sight to direct its unusual activity as it "flies" on the water for considerable distances by flapping its valves and expelling water from the apertures near the fringe. Even if this is not so, the experiments of Wenrich (1916), who determined the smallest white card which produced a shell-closing response in this scallop, showed that the animal was extremely sensitive to minimum changes in brightness. On the other hand, in abyssal or underground Molluscs, visual organs tend to be less elaborate, and vision takes a secondary or negligible place in the creature's activities.

*Pecten*

Snails have been trained to negotiate a T- or Y-maze (Garth and Mitchell, 1926; Fischel, 1931; Brandt, 1935), while a number of Molluscs demonstrate a remarkable ability to seek their habitual homes from a distance.¹ The mechanism employed is unknown; an association of several senses is possibly involved among which touch probably figures largely and vision little if at all.

CEPHALOPODS are visually in a very different class. There can be little doubt that they use their eyes for the actual observation of objects and in this respect, depending on vision rather than smell, they are unique among Molluscs. Functionally their eyes are capable of a considerable degree of pattern-vision, they have a good perception of movement, and have adaptive and accommodative powers. They are the only Invertebrates which exhibit pupillary reactions remotely resembling those characteristic of Vertebrates (Magnus, 1902); these reactions are most readily excited by yellow-green light of the same spectral range which induces the most active phototactic responses. Although many Cephalopods change their integumentary colour to harmonize with their background by reflexes originating in the eyes,² Carl von Hess (1921-22) found no evidence to suggest that colour vision is present; and the positive claims made by Goldsmith (1917), Bierens de Haan (1926), Tinbergen (1939) and Kühn (1930-50) that, as judged by behavioural experiments, they can differentiate hues are open to serious criticism (Carter, 1948).

The visual capacity of *Octopus* has received a considerable amount of attention by such writers as von Uexküll (1905), Polimanti (1910), Goldsmith (1917), ten Cate and ten Cate-Kazejewa (1938), and particularly by Boycott and Young (1950-56) and Young (1956). The standard lay-out of their experiments was to allow an octopus to attack and eat a crab associated with a particular geometrical figure, but to

*Octopus*

¹ *Chiton*, Pelseneer, 1935; the limpets, *Patella* and others, Davis, 1885-95; Lloyd Morgan, 1894; H. Fischer, 1898; Piéron, 1909; Thorpe, 1956; the littoral Pulmonate, *Onchidium*, Arey and Crozier, 1918.

² p. 93.

punish it with an electric shock if it attempted to attack a crab associated with another figure. In such experiments the octopus is eminently trainable. The form vision of the animal is surprisingly good. It can distinguish a square of 4 cm. from a square of 2 or 8 cm., between a square and a rectangle of equal area, and between figures of various orientation such as three sides of a square, an L, a vertical or horizontal line, a cross, and so on ; curiously it was found that difficulties were experienced in differentiating oblique lines or a circle from a square. Further, a square of 4 cm. was not confused with a square of 8 cm. at twice the distance, a differentiation which indicates some spatial perception.

The facility of *Octopus* in learning to differentiate between horizontal and vertical lines and its relative difficulty in differentiating oblique lines or such figures as a diamond and a triangle, suggested to Sutherland (1957) and Dodwell (1957) that the vertical and horizontal axes have a special status in the discrimination of shape. On this basis Sutherland advanced a theory that the output from the visual cells of the octopus was so projected in the optic lobes as to correspond with a vertical and horizontal system of coordinates ; they would thus correspond with the fundamental coordinates of orientation in space—the vertical depending on gravity and the horizontal aligned to the visual horizon.¹ This hypothesis would account for some similar experimental results obtained by Fields (1932) and Lashley (1938) on the sense of discrimination in rats ; and it is also interesting that in man, reference to vertical and horizontal components seems to be of primary importance, in association, of course, with other systems of coordinates, in referring a point in the environment to the centre of the visual field.



Sepia

Somewhat similar visual reactions can be elicited in the cuttlefish, *Sepia* (Sanders and Young, 1940) ; and the perception of movement by this mollusc is good with an optimum angular velocity of about 7° per sec. (Boulet, 1954). Indeed, it would seem that *Sepia* is in some ways more amenable to training than *Octopus* ; if a prawn is presented as prey and placed behind a transparent glass partition, the former will desist attacking after several attempts while *Octopus* will persistently swim straight into the screen ; moreover, the cuttlefish will pursue a prawn visually round a corner, while *Octopus* will give up the hunt unless the invisible prey is reached and can be touched by its exploring tentacles (Sanders and Young, 1940 ; Boycott, 1954) (Fig. 730). It would seem, therefore, that the two species vary considerably in their dependence on vision for hunting. It would appear, also, that the former possesses considerable intelligence in that it can pursue its purposes by indirect means and shows some capacity for learning.

There seems little doubt, however, that these capacities have been exaggerated. Pliny—that prolific purveyor of intriguing inaccuracies—in his

¹ p. 669.

Natural History described how *Octopus* would insert a stone between the open shells of a bivalve so that the soft mollusc could be devoured at leisure, an observation repeated by Jeannette Power (1857) to demonstrate the importance of vision in the behaviour of this creature. In her aquarium, she wrote, an octopus holding a fragment of rock in one of its arms, intently watched the lamellibranch, *Pinna*, until it opened its valves. As soon as these were fully opened, she reported that with incredible address and promptitude the octopus slipped the stone between the valves so that they could not close again, and thereupon set about devouring its victim.¹ Piéron (1909) claimed that Octopods were able to uncork a bottle in order to obtain crabs seen through its glass walls; and other somewhat similar statements appear in the semi-scientific literature. In view, however, of the apparent inability of the octopus to use a "tool," it may well

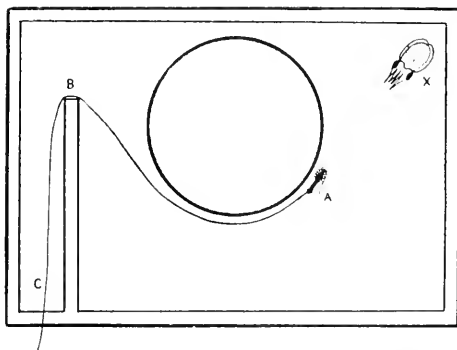


FIG. 730.—THE HUNTING CAPACITY OF *SEPIA*.

Within a tank the cuttle-fish is situated at X. In the tank is a circular opaque bucket and an opaque enamel plate. A prawn to which is attached a long thread is placed at A within sight of the octopod. As soon as its attention had been drawn to it and it had begun to follow the prawn, it was pulled by the thread to position B behind the opaque bucket. The octopod followed, whereupon the prawn was pulled behind the opaque plate to C, again out of sight of its pursuer. The latter would follow around B and thereupon it was allowed to devour its prey (Sanders and Young).

be that such stories are fairy tales or that the incidents were determined rather by chance than by purposive behaviour (Boycott, 1954).

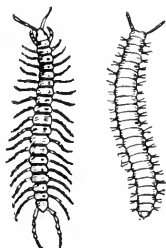
THE VISION OF ARTHROPODS

ARTHROPODS are a phylum so large and amorphous that a study of the visual perceptions of the various types must be taken separately; this diversity in function follows from an equally marked diversity in habit and is to be expected within a group which contains members smaller than some Protozoa with great simplicity in organization, and others (particularly Insects) which are rivalled in their visual capacity and learning ability only by the higher Mammals. Apart from Insects, however, relatively little is known of the visual

¹ A somewhat similar story was recorded by Leonardo da Vinci (Manuscript H 14) who described how crabs inserted a stone or twig into the open shell of an oyster.



Onychophore,
Peripatus



Centi-
pede
pede
(Myriapods)



Daphnia



Lobster



Leander

performance of Arthropods. Among the lower types the tactile sense takes pride of place in biological utility; in Insects vision is dominant with the sense of smell (centred in the antennae) a good second.

The ONYCHOPHORA are provided with eyes which merely differentiate the presence or absence of light from which the creature persistently flees. A crude image-formation is possible among the MYRIAPODS; although *Lithobius* is trainable to the extent that it can master the single turn of a simple T-maze, it does so by its tactile sense on the basis of the texture of the walls (Scharmer, 1935). The visual sense of the smaller CRUSTACEANS is almost certainly similarly crude, but light perception at any rate, with phototactic responses while swimming is well developed. In the Cladocera, particularly the water-flea, *Daphnia*, it has been established by a large number of observers that the phototactic response varies with the wave-length of light so that a differential sensitivity would appear to exist, particularly affecting red and blue.¹ Moreover, an elementary degree of training is possible even in these minute creatures since the positive taxis of *Daphnia* to a source of light through a narrow tube can be rendered less clumsy with experience (Blees, 1918); but any such feat as the negotiation of the single turn of a T-maze seems to be beyond the capacity of the small Crustaceans (*Daphnia* and *Simocephalus*, Agar, 1927). These creatures thus seem to be inferior to earthworms in this respect.² Some directional sense to light stimuli is probable, and Exner (1891) suggested that the Copepod, *Copilia*, made the most effective use of its simple ocular apparatus, by scanning movements of the stalk-like eye controlled by its system of muscles (Fig. 139).

Not much more is known about the visual functions of the higher Crustaceans, although the anatomical elaboration of their compound eyes with their complex nervous connections would indicate visual potentialities of considerable proficiency. In the lobster, for example, optomotor reactions are readily elicited when the animal is confronted with a black-and-white striped rotating drum³; moreover, reactions differ depending on the colour of the stripe, suggesting the presence of a colour sense or, at any rate, a differential reflex action to different wave-lengths of light.⁴ Many of these animals, however, are essentially nocturnal or frequent ocean depths where the paucity or absence of light must preclude acute vision. It is probable, indeed, that as determinants of behaviour the eyes are of secondary importance to the

¹ v. Frisch and Kupelwieser (1913), Ewald (1914), Koehler (1924), Eckert (1935), Heberdey (1936), Heberdey and Kupka (1942), Smith and Baylor (1953). It is to be remembered that these differential responses may be served by different mechanisms—the dermatoptic and the ocular.

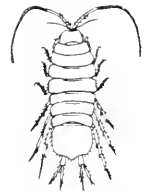
² p. 573.

³ *Homarus*—v. Buddenbrock *et al.* (1952).

⁴ Schlieper (1926–27), Kästner (1949) in the crab, *Carcinus*, the shrimp, *Crangon*, the prawn, *Leander*.

sensory bristles which are distributed all over the body and appendages, particularly the antennæ. These are of two types, being sensitive to touch or chemical stimuli, and are present in enormous numbers ; in the lobster, for example, there are said to be 50,000 to 100,000 on the pincers and walking legs alone.

A considerable aptitude to training is evident among the Malacostraca but it is based on the tactile sense rather than on vision ; the feat of mastering a T-maze is easily acquired by those species which have been investigated but the aptitude is based on the texture of the walls (Agar, 1927 ; Gilhousen, 1929 ; ten Cate-Kazejewa, 1934 ; and others), and is equally shown by the blind Isopod, *Asellus* (Bock, 1942).



Asellus

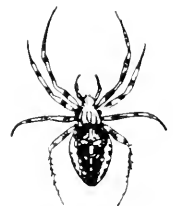
THE VISION OF ARACHNIDS

The function of the eyes of ARACHNIDS is very variable and often crude. The smaller species (Acarines) merely respond to the intensity of light, and training experiments with water-mites (Hydracarina) utilizing any sense have been unsuccessful (Agar, 1927). The larger representatives, however, have more fully developed visual functions. The jerrylanders have relatively good vision ; but with the exception of spiders the other Arachnids probably only perceive variations in the intensity of light and movement ; the optics of their ocelli is poor and the number of visual cells small, while visual impressions seem to play an insignificant part in their behaviour.

THE VISION OF SPIDERS has received more attention than that of any other type (Petrunkévitch, 1907-11 ; Homann, 1928-53 ; Millot, 1949 ; Drees, 1952). It is true that the web-spinners with their rudimentary ocelli of a short effective visual range are not particularly visually conscious, for their behaviour is dominated essentially by their exquisite sense of touch ; any tremor on the web caused by an alighting insect excites their immediate attention, probably while the object causing the tremor is still out of the range of their vision. It is interesting that this sense of vibrotropism is purely reflex, for photography has shown that the waiting spider orientates itself so that the vibrations of the web stimulate the legs on each side equally and then sets out in a straight path for its victim. Similarly, ripple-spiders sit at the water's edge resting their forelegs on the surface waiting to appreciate the ripples set up by an alighting insect. In the same way the vibrations of a tuning fork on the web or in the water will excite the spider to run out as if to capture prey. The more active hunting types, however, which move abroad to chase their prey, base their behaviour progressively upon vision, each element in the ocellar system having a particular function and the whole acting in a curiously reflex manner.



Jerrylander



Web-spinner,
Aranea



Wolf-spider,
Lycosa

*Evarcha blancardi*

The behaviour of the jumping spider, *Evarcha blancardi*, the arrangement of the ocelli of which is shown in Fig. 216, may be taken as an example. It sees its prey (or mate) with the posterior lateral eyes which, situated far back on the head, have a wide field of vision and respond to moving stimuli only; a stationary object excites no reaction. As the image of the moving object crosses the retina of these ocelli, the spider reflexly turns its body in the direction of the object with the result that the image falls on the retina of one of the anterior lateral ocelli, whereupon a further turning movement throws the image on both anterior lateral ocelli and the two central ocelli. If the former ocelli are covered, this second turning movement does not occur. It would seem that the function of these ocelli is to judge distance binocularly, that of the central ocelli, which have a small field and a short range, to perceive the form of the prey; in each the lens is capable of forming sharp images. A male, for example, acts as if it can distinguish between a female of its own species or a male of its own or another species at a distance of 2 to 3 cm. At a distance of 1.5 cm. it leaps upon its victim with accuracy, but if the lateral anterior ocelli are covered the distance of the leap is misjudged. The posterior lateral ocelli therefore act as the peripheral retina of man, collecting impressions from the whole visual field; the front row of four eyes acts together as the human fovea, the lateral pair being most useful binocularly at a short distance, the central pair being the chief agent for visual analysis. The small posterior median pair of ocelli, on the other hand, are used for the detection of movement behind the spider.

The reflex nature of the response is illustrated by the automatic movements of the limbs following retinal stimulation. Homann found that on covering the two median ocelli the first pair of legs was held up by the contraction of the femoral muscles and as the animal ran forwards they merely clawed the air instead of touching the ground; if one of these eyes were covered the foreleg on the blind side alone was held up and the body was tilted sideways.

Despite the apparent automatism of this reflex response, however, spiders display a very considerable degree of visual intelligence. Nowhere is this more aptly illustrated than in the stalking of a fly on a creviced wall by a jumping spider. Spying a fly settled on the wall some distance away, the spider, knowing that the attention of the fly will be excited at once by a moving object, creeps with the greatest care to the nearest crevice in the brickwork. Arrived there, knowing that the fly will soon take wing, it scampers rapidly along the crevice hidden from view until it comes within range of its victim; thereupon, anchoring itself by a life-line of silk to the brickwork, it leaps upon its victim with incredible rapidity, hoisting itself back to safety by the silken cord.

Moreover, in their visual activities a considerable degree of sensory analysis exists, for jumping spiders can be negatively conditioned to unpalatable prey, and Drees (1952) found that their form vision is sufficiently effective to allow negative conditioning by means of an electric shock to a response acquired by training to visual stimuli such as triangles and crosses. It is also of interest that the jumping spider has been shown by its response to the optomotor reaction to have a selective sensitivity to orange (Kästner, 1949), a response which may indicate some degree of "colour vision" on a reflex level.

THE VISION OF INSECTS

The mastery of a new element and the adventure of the experiences afforded by a third dimension would be expected to give a fillip to the sensory reactions of Insects, while the development of flight with the consequent ease and speed of exploring new environments must stress the importance of efficient distance receptors in the gathering of adequate data for effective orientation. These expectations have been realized ; and to Insects much the most important receptor-organs are the eyes. Indeed, in their efficiency, their capacity to resolve a pattern or to interpret movements, the eyes of Insects excel those of most Vertebrates ; moreover, alone among Invertebrates many species have a fully developed colour sense, while they have assumed a faculty apparently unique to Arthropods—the power to analyse the plane of polarization of light and orientate themselves thereby. Finally, small though the insect brain may be, and dominated though the creature is by automatic and rigid reflex reactions, it shows an amenability to learning and a power to remember unique in the invertebrate world.

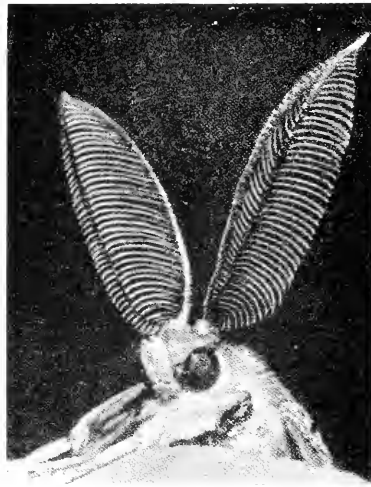


FIG. 731.—THE HEAD OF THE MOTH SHOWING THE EYES AND THE ENORMOUS ANTENNÆ (Richard Cassell).

In the behavioural activities of Insects other senses are also important.

The olfactory sense, indeed, would seem to be more fundamental than vision ; thus it has been shown by Schremmer (1941) that newly emerged specimens of the moth, *Plusia gamma*, seek flowers by scent only, this faculty being presumably innate, but that once an association with a particular flower has thus been established, further visits are determined by vision and scent. Moreover, in the recognition of their fellows and as a guide to homing when illumination is ineffective, odour is often a major determinant of conduct ; the male moth, for example, with its extremely sensitive antennæ, is said to find a female a mile or more distant by this means alone (Fig. 731) (Bonnett, 1779-83 ; Turner, 1907 ; Schneirla, 1929-33 ; Carthy, 1950 ; Vowles, 1955 ; Dethier, 1957).

The organs of smell are situated on the last 8 segments of the antennæ and consist of minute pits which are present in large numbers, sometimes up to a thousand on a single joint. The taste organs occur not only on the mouth and labial palps but also sometimes on the antennæ and the feet. The sense of touch is subserved by minute hairs associated with the antennæ, the maxillæ and the face ; the setæ are non-living but each has a sensory cell at its base with nervous connections. Many species are without ears but they are certainly well developed in insects capable of producing sounds : when they are present each

ear consists of a pit filled with air or fluid across the opening of which is stretched a drum-like membrane. In some Orthoptera the ears are on the shanks of the front pair of legs or on the sides of the abdomen above the base of the third legs; in others on the first segment of the body; in blow-flies under the bases of the wings; in gnats on the bases of the antennæ; and so on. In all the sense organs there is a considerable variation between species, while there may well be one or more types of sense organs with which we are not familiar that have no counterpart in the vertebrate sensorium.

The visual function of the *LARVÆ OF INSECTS* is relatively crude, a necessary corollary of the simplicity of the structure of the stemmata. In the more simple forms a crude sensitivity to light is the only possible response, but in the more elaborate forms, particularly when the eyes occur in groups, a coarse mosaic imagery with some degree of form vision is possible.¹ It may well be that the pendular movements of the anterior part of the body exhibited by so many caterpillars are an expedient to mediate form vision by scanning movements with the simple apparatus available, the visual impressions being perhaps coordinated with proprioceptive stimuli derived from the motion. The entire group of stemmata functions as a unit and if all are covered except one, form perception is lost and only phototactic responses remain (Friederichs, 1931; Dethier, 1942-43). The fact that the caterpillars of butterflies (*Vanessa*) are attracted by green leaves or paper of the same colour suggests the possibility of a crude colour sense (Götz, 1936). Finally, the stemmata of some species are capable of utilizing the pattern of polarization of light as a means of orientation.²

The function of the *DORSAL OCELLI OF ADULTS* is more problematical; since their principal focus does not coincide with the retinal plane, they are ill-designed for image-formation although well adapted to admit light (Homann, 1924; Wolsky, 1930-31; Cornwell, 1955). Any capacity for the perception of form is therefore probably negligible. In view of the facts that some insects with only their ocelli uncovered behave as if blind and that the reflex responses of the compound eyes to light are less rapid when the ocelli are covered, it has been suggested that the ocelli are stimulatory organs which accentuate, although they do not initiate, phototactic responses.³ In other species, however, they have been shown to participate fully in the activities of the animal,⁴ while they are the only effective organs in those species in which compound eyes are lacking.⁵ Moreover, it was shown by Wellington (1953) that the ocelli of the flesh-fly, *Sarcophaga*, are sensitive to



Caterpillar

*Sarcophaga*

¹ Larvæ of the tussock-moth, *Lymantria*—de Lépiney (1928); of the beetle, *Cicindela*—Friederichs (1931).

² Saw-fly, butterfly—Wellington *et al.* (1951), Wellington (1953) (p. 66).

³ In ants—Homann (1924); bees—Müller (1931); the fly, *Drosophila*—Bozler (1925), Parry (1947), Cornwell (1955).

⁴ In the bug, *Cryptotympana*—Chen and Young (1943); the flesh-fly, *Sarcophaga*—Wellington (1953).

⁵ p. 221.

changes in polarized light and thus aid in orientation. In the locust, illumination of the compound eye produces on- and off-spike potentials in the ventral nerve cord, of the ocelli off-responses only (with perhaps a very brief on-response, Hoyle, 1955); the former responds to movements of an external object while the latter does not (Burt and Catton, 1954-56). It would thus seem obvious that the function of the ocelli of Insects varies in different types depending on such factors as the degree of development of the compound eye and the habits of the species.

*Locusta*

THE COMPOUND EYES OF INSECTS, on the other hand, possess functional attributes of a high order which have been extensively investigated¹; their appreciation of light and colour as well as form, movement and spatial relationships compares well with that of many types of Vertebrates. Moreover, in some insects the compound eye, occasionally in addition to the ocelli, can appreciate changes in the polarization of light.²

More study has been devoted to the function of the compound eye of Insects than to the eyes of any other Invertebrate. The two classical methods of approach³ have been adopted—behavioural experiments and reactions based on the electro-physiological characteristics of the eye on stimulation by light. The first is the more informative in that it gives some idea of the sensations appreciated by the insect concerned, but insofar as many insects are untrainable perhaps because of their automatism, perhaps because of lack of intelligence, the method is by no means universally applicable. It is always to be remembered, of course, in interpreting the results of the second method, that physiological responses on a reflex level need not necessarily ascend into the level of consciousness and can only be translated with the greatest reserve into terms of sensation.

Behavioural experiments depending on the laying down of conditioned reflexes can be made available for the investigation of the responses of many insects; the honey-bee, *Apis*, for example, can be trained to go to a container with sugar placed beside a black disc and avoid one marked with a black cross (v. Buddenbrock, 1937). Unconditioned reflex responses such as the optomotor reaction to black and white stripes on a moving drum are also readily elicited in many insects. Again, the honey-bee is very sensitive to stimulation of this type, responding if stationary by a reflex sideways movement of the head and thorax; if it is crawling it makes a sudden change of direction opposite in sign to that of the movement of the environmental pattern. In similar circumstances the fruit-fly, *Drosophila*, will completely

*Apis**Drosophila*

¹ See among others, Eltringham (1933), v. Frisch (1950), Wigglesworth (1953).

² p. 66.

³ p. 568.

reverse its direction of movement, a reaction repeated with dramatic precision on each occasion and in rapid succession on repeated stimuli. If the field is kept stationary a moving insect shows the same type of response to the shift of the retinal image produced by its own movement (v. Buddenbrock and Moller-Racke, 1952).

The *electro-physiological characteristics* of the visual mechanism have recently been applied with considerable success to the physiology of the compound eye. Depending on the type of electrical response on stimulation by light, two distinct physiological types have been differentiated by Autrum and his co-workers (1948-53).

(1) *FAST EYES*, found in rapidly flying diurnal insects (the blow-fly, *Calliphora*, the bees, *Apis* and *Bombus*, the wasp, *Vespa*, and so on). On stimulation by light the electro-physiological characteristic of such an eye is a diphasic wave made up of an initial positive response indicating the on-effect, followed by a terminal negative response indicating the off-effect; on prolonged stimulation the initial positive response subsides rapidly. In such an eye there is a high temporal resolution with a response to intermittent stimulation in the form of flicker up to 250 or 300 stimuli per sec. The absolute threshold of sensitivity to light is, however, high; the reaction is little affected by light- and dark-adaptation; and the optomotor response shows an ability to discriminate between stimuli of 200 per sec.

(2) *SLOW EYES*, seen in nocturnal, aquatic or slow-moving insects such as the grasshopper, the water-beetle, *Dytiscus*, and cockroaches (as well as *Limulus*). Such an eye is characterized by a low threshold of flicker to intermittent stimulation up to 40 to 50 per sec.; the absolute threshold of sensitivity is low; the reaction changes markedly in light- and dark-adaptation; and the subjective optomotor response can be obtained only by stimuli up to 5 to 10 sec.

The experimental evidence makes it probable that the characteristic properties of these two types of eye are attributable more to the central neurones than to the end-organ, particularly to the first optic ganglion¹ (Autrum, 1951-54; Autrum and Gallwitz, 1951). The optic lobes of both types are the source of spontaneous electrical oscillations² elicited by the onset or cessation of stimulation; in the slow type of eye the frequency of these rhythms lies between 20 and 35 cycles/sec.; in the fast type, between 120 and 160/sec. (Adrian, 1937; Roeder, 1939-40; Crescitelli and Jahn, 1942; Massera, 1952; Autrum, 1952; Burkhardt, 1954), and it is noteworthy that the fast type can be converted into the slow type by the surgical removal of portions of the optic lobe (Autrum and Gallwitz, 1951; Autrum, 1951-52).

In general, insects respond to the short waves of the spectrum rather than to the long. The cornea (of the bee, *Apis*, and the flesh-fly, *Sarcophaga*) is transparent to wave-lengths as short as 253m μ , the



Bombus



Vespa



Dytiscus



Cockroach

¹ p. 524.

² p. 524.

tracheal tapetum fluoresces in ultra-violet light and it would seem probable that the retinal cells are sensitive to rays of this type (Lutz, 1924-33; Bertholf, 1930-32; Lutz and Grisewood, 1934; Carter, 1948). Photo-negative insects such as the ant thus take shelter from ultra-violet light unseen by the human eye (Lubbock, 1885; Forel, 1886) and light-seeking insects such as moths and bees are attracted by it (Fig. 732) (Lutz, 1924-33; Lutz and Grisewood, 1934). On the other hand, although some species¹ undoubtedly respond to red (up to 690 m μ), most are not attracted by this colour because of the high threshold but treat red as black.²

In optomotor experiments when dark and light grey stripes are



Ant



Moth

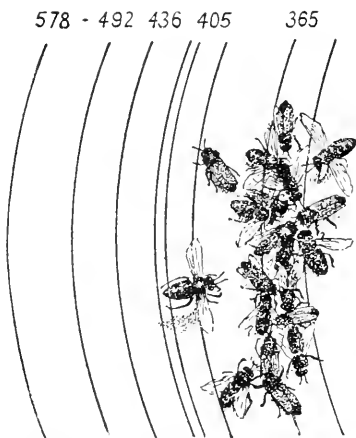


FIG. 732.—THE SPECTRAL SENSITIVITY OF THE HONEY-BEE.

Indicating the attraction of the ultra-violet part of the spectrum. The numbers indicate wave-lengths in m μ (Tinbergen, after Kühn).

used, the *discrimination of luminosity-differences* is found to be generally low—about 20 times lower in the bee than in man, and in some other insects poorer still (Wolf, 1933; Hecht and Wald, 1934; v. Buddenbrock, 1935; Hundertmark, 1937-38). When coloured light is used as a stimulus it is found that the most effective parts of the spectrum are generally in the yellow-green and ultra-violet, particularly the latter (Fig. 733).³ The spectral location of the first region corresponds closely to the peak of the luminosity-curve in man, the variation in some insects resembling the human dark-adapted state (*Apis*) and

¹ Such as butterflies (*Pieris*, *Vanessa*—Ilse, 1928), fire-flies (*Photinus*—Buck, 1937) and locust hoppers (*Locusta*—Chapman, 1954).

² The honey-bee, *Apis*—v. Frisch (1914), Kühn (1927); the wasp, *Vespa*—Schrenkner (1941).

³ 553 m μ in the yellow-green and 365 m μ in the ultra-violet for the bee, *Apis*, (Bertholf, 1931-32; Sander, 1933; Weiss *et al.*, 1941-43; and others). 540 m μ for the equal energy spectrum in *Drosophila* (Médioni, 1956). The same applies roughly to Crustaceans (p. 578).

*Calliphora*

in others the human light-adapted state (*Pieris*) (Schlieper, 1927-28 ; Ilse, 1932). The electroretinogram obtained on stimulating the retina with different wave-lengths also shows a curve resembling the absorption-curve of visual purple in Vertebrates (the grasshopper, *Melanoplus*—Jahn, 1946). The occurrence of a Purkinje shift towards shorter wave-lengths in decreasing intensity of light in some insects suggests the presence of two receptor mechanisms (*Drosophila*—Fingerman and Brown, 1952-53) ; in this connection the presence of twin-peak sensitivities in electroretinograms is also of interest (at 630 and 540 $m\mu$ in *Calliphora*—Autrum and Stumpf, 1953). These, of course, are measurements of the threshold of physiological response, not of sensation.

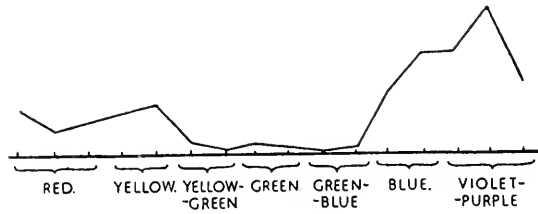


FIG. 733.—COLOUR VISION IN INSECTS.

A chart showing the relative number of visits of *Gonepteryx rhamni* to papers of different colours during the feeding phase (after Ilse).

The capacity for *colour vision* in insects has given rise to some controversy. It would seem reasonable to suppose that the brilliant colours of flowers would be ecologically linked with the insect visitors on which so many plants depend for their propagation. Such a suggestion demands that flower-visiting insects, which reciprocally depend on the flowers for their food, should appreciate and differentiate the variegated riot of colour evolved for the mutual benefit of both. It must not be thought, however, that colour vision in insects is confined to those that visit flowers or that its function has been evolved specifically for this purpose and none other ; the flower-visiting beetle, *Cetonia*, for example, is colour-blind, whereas the dung-beetle, *Geotrupes*, is endowed with a well-developed colour sense. However that may be, it has long been accepted for this reason that most insects are possessed of colour vision. The first to extricate this problem from the vagueness of speculation and subject it to scientific analysis was Sir John Lubbock (1885) who applied the relatively simple but somewhat inconclusive technique of "preferential choice."¹ On exposing honey on coloured cards and recording the frequency with which each was visited, he found that the honey-bee exhibited a substantial degree of colour differentiation with a marked preference for blue. At a considerably

*Cetonia**Geotrupes*

¹ p. 568.

later date, however, Carl von Hess (1913) concluded on the basis of similar experiments that this insect moved towards different lights depending on their relative intensity and that it was colour-blind ; but von Frisch (1914–50), in a long series of well-controlled experiments wherein other factors were excluded, confirmed Lubbock's original conclusion and demonstrated that, after training, the bee reacted selectively when presented with sugar-water associated with differently coloured squares on a checkerboard, preferring blue and yellow to other hues. These results were corroborated in the bee by Kühn and Pohl (1921) and Kühn (1927), who used pure spectral colours, and by various techniques in other species (Fig. 733).¹

The results of the earlier investigators gave the impression that the bee was only able to distinguish between two groups of colours, the yellow group and the blue-violet group ; but although this applies in a general way to their reaction to the colours of flowers in nectar-hunting, it was later demonstrated that this insect was able to distinguish several colours within each group if trained to show differential responses (Lotmar, 1933). Thus after training to bands of spectral light, bees have been found to distinguish four regions : 650–500 $m\mu$ (red-green), 500–480 $m\mu$ (green-blue), 480–400 $m\mu$ (blue-violet), and 400–310 $m\mu$ (ultra-violet), the last being probably perceived as a colour (Kühn, 1927 ; Hertz, 1939). At a later date Daumer (1956) interpreted the reactions of bees as mediated through 3 types of receptors—yellow, blue, and ultra-violet. Red flowers seem to be distinguished because of their reflection of ultra-violet. The colour system of the bee is therefore widely different from that of man.² Moreover, on testing optomotor reactions, von Buddenbrock and Moller-Racke (1952) concluded that butterflies have three receptors—an orange-red, a yellow and a green-blue. It would thus appear that different species have different types of colour vision (Ilse, 1928–49 ; Schleghtendal, 1934), while some may be colour-blind.³ Finally, various regions of the compound eye may react differently : thus the antero-ventral portion of the eye of the water-boatman, *Notonecta*, is equally sensitive to all colours while the dorso-posterior part shows preferential differences in colour-sensitivity (Lüdtke, 1938–54 ; Rokohl, 1942 ; Resch, 1954).

It is interesting that different mechanisms are applied in different activities since innate reactions show a selective responsiveness to very different stimuli ; one reaction may be released by the intensity of light, another by its wave-

¹ The bee-fly, *Bombylius*, and the hawk-moth, *Macroglossa*—Knoll (1925–26) ; butterflies, *Pieris*, *Gonepteryx* and *Vanessa*—Ilse (1928), Timbergen *et al.* (1942) ; the aphid, *Myzus*—Möricke (1950) ; the fruit-fly, *Drosophila*—Fingerman and Brown (1952–53).

² And also different from that of birds which are attracted preferentially to red flowers (p. 630).

³ Such as the nocturnal stick-insect, *Dixippus*, and the bug, *Troilus* (Hundertmark, 1936–37 ; Schleghtendal, 1934).



Bombylius



Dixippus



Notonecta

length; in one response the bee may act as if colour-blind, in another as if partially so, and in a third it may show a wide discrimination of hues. In the same way the hawk-moth, *Macroglossa*, selects yellow and blue objects when hungry, yellow-green backgrounds for oviposition, and dark surroundings of any colour for hibernation (Knoll, 1925-26). This restriction of a specific response to a few "sign-stimuli" rather than to all possible environmental clues is of wide application; it is well exemplified in the apparent blindness of the water-beetle, *Dytiscus*, in its hunting reactions¹ and is by no means confined to Insects.²



Musca



Butterfly, *Vanessa*

The perception of form in insects appears to be rudimentary. The visual acuity as measured by responses to revolving striped drums is relatively low (Hertz, 1929-39; Hecht, 1931)—about 1/100 that of man in the bee, 1/1,000 in *Drosophila* (Baumgärtner, 1928; Hecht and Wolf, 1929; Hecht and Wald, 1934; Gavel, 1939; Roeder, 1953), while in the house-fly, *Musca*, the narrowest stripe that can be perceived subtends an angle of 5° (Gaffron, 1934) (in man, 1'). These results of behavioural experiments correspond with the theoretical acuity deduced from the structure of the eye (Pütter, 1908; Best, 1911).³

As would be expected from their low standard of visual acuity, the capacity of insects to analyse a pattern is relatively poor. It is true that experiments have shown that bees and butterflies can be attracted by broken or checkered figures and divided contours to which they have been trained, a response which confirms the biological value of "honey guides" on flowers (Zerrahn, 1933; Hertz, 1935; Bolwig, 1938).⁴ It is also true that the honey-bee can be trained to seek a sugar-container associated with a black disc and avoid one associated with a black cross or can differentiate four parallel lines from a black circle; but it cannot be conditioned to distinguish between a black cross and four parallel lines on a white surface (von Buddenbrock, 1952). In order to allow the discrimination of patterns, therefore, the differences must be gross. It is probable, indeed, particularly in so far as the "fast" type of eye is concerned, that the response is less to the recognition of the configuration of objects than to the frequency of change of retinal stimulation (Wolf, 1933-37) and that fast-flying diurnal insects resolve the spatial display of a pattern into a temporal display of sequential stimuli. The method of interpretation of slow-moving, nocturnal or aquatic insects is not yet known.

From these characteristics it follows that moving objects excite

¹ p. 103, Fig. 74.

² p. 664.

³ p. 171.

⁴ It must not be thought that all the adult bee's activities in visiting flowers for honey are determined by vision. At relatively close quarters the sense of smell is important. Bees can be trained to react to scent alone. Moreover, when the insect lands on the flower, taste-organs which occur not only on the mouth but on the antennae, labial palps and feet, come into play. In the search for honey, therefore, the antennae are the distance-receptors, the organs of smell the intermediate, and of taste the contact-receptors. See Bolwig (1954) and others.

attention and stationary objects tend to be neglected. This tendency is borne out, as we have already seen¹ in behavioural experiments involving the optomotor response to a striped drum which shows a high flicker-threshold up to 200 per sec. in the bee,² the corresponding figures in man as measured by the fusion frequency of flicker being 50 to 100 depending on the intensity of illumination and the size of the field stimulated (Collins and Hopkinson, 1954); similarly, the fusion-frequency as measured by the changes in the electrical potential of the retina in many insects, particularly of the rapidly flying diurnal type, may reach very high values,³ a capacity doubtless correlated with the need to resolve succeeding impressions during flight. It would thus seem that in their activities insects depend much more on the primitive faculty of the appreciation of movement than of form. The widely over-lapping visual fields of the compound eyes allow *perception of distance*, a power of judgment which is impaired if one eye is obscured (Homann, 1924); and behavioural experiments show that a high degree of *spatial appreciation and localization* is possible (Tinbergen, 1932-38; Wiechert, 1938). The extraordinary capacity of some insects for memorizing and recognizing landmarks in their territory has already been discussed at length.⁴

The dependence of insects on visual stimulation by moving objects is seen in the every-day behaviour of the ordinary house-fly which neglects stationary objects but immediately absconds on the first suggestion of movement. It is also exemplified in a striking way by the habits of the praying mantis (Fig. 734);



FIG. 734.—THE PRAYING MANTIS, *MANTIS RELIGIOSA*

Sitting on a leaf. Note the large and prominent eyes and the "praying" position of the front legs. The terminal part of the bent fore-leg with its powerful joint resembles a pen-knife, normally held half open ready to snap shut against its "sheath" with the prey trapped between (photograph by Michael Soley).

¹ p. 583.

² 60 stimuli per sec. in *Aeschna* nymphs, Sälzle (1932), and in *Anac* nymphs, Crozier *et al.* (1937); see also Autrum and Stöcker (1952), Autrum (1954).

³ 95 per sec. in the ocellus of the bee (Ruck, 1954) and of the order of 165-300 stimuli per sec. in the compound eye of this insect, or 265 per sec. in the blue-bottle *Calliphora* (Autrum and Stöcker, 1950; Autrum, 1952). Corresponding measurements in man with the electroretinogram are 25-30 for the scotopic and 70 for the photopic fusion frequency (Wadensten, 1956).

⁴ p. 78.

the adjective, incidentally, applies not to the habits of the insect but to its characteristic stance with its front legs raised as if in an attitude of prayer. The female is a particularly anti-social creature who will eat anything in sight, including her mate. Since she can only see moving objects, the male approaches her with staccato movements, standing motionless whenever she looks in his direction, exactly in the manner of the children's game, Grandmother's Footsteps. Fortunately, the male has better vision than the female and usually manages to approach her in this cautious manner until he can leap upon her; but the end is usually the same because he is generally eaten either while mating is in progress or after it is finished.

ACCOMMODATION IN INVERTEBRATES

The relative simplicity of the eyes of Invertebrates would not lead us to expect elaborate accommodative facilities; from the functional point of view, of course, the degree of visual acuity of most types would not merit a complicated mechanism of this nature. In rare cases a muscular apparatus provides an active method of accommodation somewhat analogous to that characteristic of Vertebrates. An exceptional device is a forward movement of the lens by increasing the contents of the globe by secretory activity. More often, however, any accommodation that is present is static in nature and depends on the provision of different optical systems in the same eye or in different eyes, one being adapted for distant vision and the other for near.



Cephalopod,
Loligo

An active muscular apparatus to produce an accommodative change of focus is seen in its most elaborate form mainly among Molluscs; it acts primarily by compressing the globe, that is, altering the position of the lens secondarily, a method of accommodation, incidentally, adopted by snakes.¹ Such an accommodative mechanism is seen in its highest form in the eyes of Cephalopods (Figs. 113, 114). Beer (1897), Heine (1908) and Pflugk (1910) considered the eyes of Cephalopods to be normally myopic (-2 to $-10D$), but v. Hess (1909) found them to be emmetropic or slightly hypermetropic. This author concluded that a considerable degree of amplitude of accommodation is effected by the forward displacement—not the deformation—of the lens, the mechanism being the relatively simple one of compression of the globe by the contraction of the ciliary muscle, an action which raises the intra-ocular pressure so that the vitreous pushes the lens forwards passively, thus producing a positive accommodation of 10 to 14 dioptries (v. Hess, 1909; Alexandrowicz, 1927); this effect can be abolished by atropine (v. Hess, 1909–12) and augmented by electrical stimulation of the cerebral ganglion (Magnus, 1902).

A somewhat similar method is seen in the Heteropod, *Pterotrachea* (v. Hess and Gerwerzhagen, 1914). The accommodation of the pulmonate, *Onchidium*, is closely allied: a muscular collar surrounds the distal part of the eye which, on contraction, alters the shape of the globe in an analogous manner. In the cockle, *Cardium*, the whole globe is invested with muscular fibres the contraction of which may serve as a similar and very primitive accommodative device.

¹ p. 648.

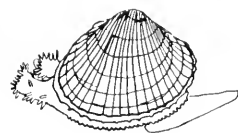
A different type of muscular mechanism appears to occur in the Copepod, *Copilia* (Fig. 139); the long slender muscle running along the side of the elongated eye may not only move this organ in different directions but also act by altering the distance between the lens and the receptor elements and thus provide an accommodative adjustment. This is reminiscent of the way in which Cyclostomes accommodate.¹

A unique method appears to be present in the elaborate eyes of certain Polychaetes such as *Aliciopa* (Fig. 112). It is said that stimulation of the secretory cell increases the volume of the "distal vitreous" lying immediately behind the lens, and it has been suggested that this pushes the lens forwards to accommodate the eye for near vision. In this eye there is in addition an accommodative muscle similar to that in Cephalopods the contraction of which should also be effective (Demoll, 1909; v. Hess, 1914).

These active mechanisms, however, are exceptional. More usually, accommodation is achieved by the static device of the presence of two optical systems in different parts of the eye. The simplest example of this is seen in the ocelli insects. In the grasshopper, for example, there is a double curvature on the proximal surface of the corneal lens which thus acts after the manner of a bifocal spectacle lens and seems to be capable of producing two images at different distances (Tümpel, 1914).

By its nature the optical arrangements of the compound eye do not admit accommodative adjustment, but this is rendered unimportant in the mosaic type of vision. It would seem, however, that the different optical configurations seen in different segments of certain compound eyes which are so arranged that in one region there are short ommatidia and powerful lenses and in another region long ommatidia and weak lenses, may provide alternative focusing mechanisms. This is seen in its most dramatic degree in composite compound eyes such as those of some Ephemeroptera and Diptera (Dietrich, 1919) and some Hemiptera (Weber, 1934) (Fig. 140), and of certain pelagic Schizopods wherein one part is adapted for near and the other for distant vision (Fig. 141) (Hesse, 1908).

Finally, two separate eyes may exist, one optically adapted for distant objects and the other for near. This is exemplified in the median and lateral ocelli of spiders,² while the same expedient is also adopted in the dorsal and ventral compound eyes of the whirligig beetle, the former being adapted for aerial and the latter for aquatic vision (Fig. 231).



Cardium



Copilia



Grasshopper



Whirligig beetle

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¹ p. 644.

² p. 580.

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FIG. 735.—CARL VON HESS (1863-1923).

CHAPTER XVIII

THE VISION OF VERTEBRATES

Of the many research workers who have given thought to the subject CARL VON HESS (1863–1923) (Fig. 735), Professor of Ophthalmology first at Marburg in 1896, then at Würzburg in 1900, and finally at Munich in 1912, did more than any other to put our knowledge of the visual behaviour of animals on a firm basis. It is true that before the period of his active work much had been done on this question, but no one up to his time had tackled this very difficult problem with the same patience, zeal and enthusiasm. It is also true that some of his conclusions are discredited today, particularly because of his habit of making sweeping generalizations from experiments which time has shown to be sometimes uncritically founded; but it is equally true that by the comprehensiveness of his work, the ingenuity of the procedures he introduced and the diligence with which he applied them, he did more than any other to excite interest in the visual life of animals and bring this subject within the ambit of science. In this field his researches covered many aspects, particularly on the mechanism of accommodation, the activities of the pupil, the light sense and, above all, the colour sense, of a number of species. Nor did his interest end in comparative physiology; in pathology, both clinical and experimental, in bacteriology and surgery his contributions to ophthalmology were immense.

The Role of Vision in Vertebrate Life

It may be surprising to us who are markedly visual creatures and whose most intimate contacts are with Mammals which appear to rely largely on vision in their ordinary activities, that the great majority of Vertebrates are much more nose- and ear-minded than eye-minded. Yet such, indeed, is the case. Even the dog lives in a colourless world of monotonies in which, it is true, form-vision and luminosity count highly, but its life is dominated to a very considerable extent by sounds which we cannot hear and scents of the acuity and diversity of which we have no conception. As we have seen to be the case with Invertebrates,¹ for the mass of Vertebrates, not only phylogenetically and ontogenetically but also in daily life, the chemo-, the tacto- and the vibratory-receptors (the lateral line of Fishes and the ears of land animals which have evolved therefrom) are more dominant than the eyes. Moreover, it must always be remembered that even those species to which vision is important, such as predators that hunt their prey, may possess visual powers very different from our own; in many, reliance may be placed almost entirely on the appreciation of luminosity and movement—not, as in Birds and Man, on visual acuity—and this may serve them well. In an attempt to reconstruct the visual world of animals it is easy to fall into anthropomorphic mistakes of this type.²

¹ Chap. XVII.

² For a fuller discussion see p. 108.

Among the pre-Fishes, the CYCLOSTOMES have little use for vision. For the greater part of their lives most of them are parasitic and, as we shall see, many of them have allowed their eyes to degenerate.¹

The activities of FISHES must be dominated largely by chemoreceptors and the vibratory receptors of the lateral line; organs of tactile sense and hearing of high acuity are also available in many species. It is true that the vast number of pelagic and surface fishes can—and do—avail themselves of vision, a fact borne out by the extraordinary anatomical development and high functional attainments of the teleostean eye, an organ capable of appreciating colour and sometimes provided with a fovea. In most other types, however, the high refractive error and the frequent absence of efficient accommodation entail a very defective visual acuity and the eye is geared essentially for the appreciation of light rather than form. Moreover, apart from a narrow belt beneath the surface, the intensity of light in the sea is insufficient for the attainment of a refined degree of form vision and even in the most favourable circumstances the amount of light reflected laterally from objects under water is meagre. In any aquatic environment vision at any great distance is impossible; in muddy or turbulent waters and in the deeps of the seas light is practically non-existent and in the clearest water is completely absorbed below a depth of 500 metres²; in the abyss darkness is absolute. Here, indeed, the only light available is created by the fish themselves by their luminous organs,³ and these, presumably, are used as social signals rather than visual aids. The activities of vast numbers of fish must therefore depend of necessity largely or entirely on the sensations of taste, smell, touch, hearing and vibration. Most fishes, in fact, live happily and apparently fully without vision even although they may be provided with excellent eyes and normally use them.

Thus the trout and other Teleosteans of mountain streams live and seem to thrive as well when the melting snows towards the end of spring convert the water to an opaque turbulence in which human vision is impossible for a distance of more than a centimetre or two; again, in the high lakes of the Alps they nourish themselves as well during the 7 or 8 months when the water is covered with a layer of ice and snow sufficiently thick to preclude all light, as they do in the months of summer. Among Selachians vision can mean little more than the perception of light and movement; even among Teleosteans vision is usually a subsidiary sense and food is recognized primarily by olfaction.⁴ A blinded fish in an aquarium may acquire his food and conduct himself in a way indistinguishable from a normal fish (the dog-fish, *Scyllium*; the ray, *Torpedo*—Verrier, 1938). Of all classes of Vertebrates, indeed, Fishes seem the least incapacitated by the deprivation of vision; the blind cave-fishes⁵ are as alert and well fed as their sighted cousins.

¹ p. 734.

² p. 722.

³ p. 736.

⁴ See p. 660.

⁵ p. 725.

This is not, however, to say that vision among Fishes is useless. When it can be utilized it is of immense biological value and occasionally it reaches a high standard, although never equal to that found in Birds or Primates. Indeed, it would seem, as Herter (1953) suggested, that the visual capacity of many fishes is so high that it cannot be adequately utilized in their natural life—an example of a wide generalization that the sensitivity of a sensory mechanism is usually greater than is justified by the apparent biological importance of the stimuli concerned, a tendency which perhaps allows the fullest efficiency at the normal level of stimulation.

When Vertebrates left the water to seek life on land, the better optical medium provided by air allowed a higher standard of vision. Among AMPHIBIANS, all the Apoda and many of the Urodeles remained in lightless surroundings, living a secretive sluggish life at a low potential, burrowing in the earth or in mud or under flat stones in shallow water; these have ill-developed eyes and base their activities to a negligible degree upon vision. On the other hand, the more active Amphibians rely largely on their eyes, and in the Anurans vision is well developed; frogs, indeed, are essentially visual animals, catching their food and recognizing their mate some distance away by vision (Banta, 1914). This tendency becomes greater in REPTILES. Even among the turtles, the most primitive Reptiles extant, vision is the dominant sense; it is less important among the Crocodilians but eminently so among lizards. The visual activity and accuracy of the chameleon as it catches insects with its bifid tongue is proverbial; in this otherwise sluggish animal the eyes, indeed, are the only organs to show obvious activity. Yet most Reptiles rely to a large extent on other senses. Thus snakes and lizards follow a trail, either of prey or their mate, by smell, the flickering tips of the tongue picking up odoriferous particles from the ground and transferring them to the extremely well-developed Jacobson's organ in the roof of the mouth where they are smelt and tasted. The rattlesnake, *Crotalus*, for example, readily recognizes and viciously attacks the king-snake, *Lampropeltis*, and will do so with equal efficiency and zest when blindfolded; deprived of his tongue, however, which removes an essential part of his olfactory mechanism, he is unable to recognize his enemy by visual clues alone and remains passive. Similarly nocturnal snakes, which have particularly good olfactory powers, can locate and strike their prey entirely without the use of vision. Apart from the visually alive arboreal types, snakes are probably alerted not so much by vision as by the conduction of ground vibrations to the inner ear through the lower jaw with which the single bone corresponding to the aural ossicles of man connects; while the sensory facial pits of some species such as crotalid vipers locate warm-blooded prey by radiant

heat with astonishing accuracy even when the snake is blindfolded or in total darkness.¹

The general tendency to rely increasingly upon vision, however, becomes much more marked in BIRDS among which the sense of vision comes fully into its own ; with the other senses poorly developed, particularly olfaction, the intense activity of bird-life is dominated almost entirely by visual impressions and their eyes can attain an order of excellence unmatched in any other species not excepting man.



FIG. 736. — THE GIANT ANT-EATER, *MYRMECOPHAGA TRIDACTYLA*

Note the very small eyes and the long exploring tongue which takes over the visual functions in seeking out ants in their nest (Zool. Soc., London).

It is only because the brain of the bird is so much inferior to that of the higher Mammals that its visual interpretation may be less effective.

MAMMALS are in a different case. The early Mammals, small and generally timid creatures leading a restricted life of nocturnal habits, derived from an ancient reptilian stock, had little use for vision even although in them for the first time the structural basis for conjugate eye-movements became laid.² In Monotremes, nocturnal habits in

¹ The facial pit of crotalid vipers (rattlesnake, moccasin, etc.) which responds to a difference in temperature as minute as 0.1° C between a small object and its background, shows its highest sensitivity to infra-red wave-lengths between 2,000 and 3,000 mμ ; moreover, its capacity for directional analysis is very accurate (Lynn, 1931 ; Noble and Schmidt, 1937 ; Bullock and Cowles, 1932 ; Bullock and Diecke, 1956).

² p. 7.

which vision plays a subsidiary part are on the whole retained. Marsupials and Placentals, however, have evolved into larger and more active types capable of wandering freely over the wide spaces during the day and therefore depending more and more on vision for their expanding activities. Among the Marsupials this evolution reaches its highest point in the kangaroos, and the same sequence is seen in the great placental family. To the Insectivores, the Chiroptera,¹ and the "Edentates," vision as a general rule is a subsidiary faculty; ant-eaters and armadillos, for example, gather their prey with their sticky tongues, never seeing the food they eat (Fig. 736). Even to the Rodents (with the exception of the squirrel family), mostly small creatures of nocturnal habits living near to the ground with a limited horizon, the eyes are usually the fourth most important sense-organ in day-to-day activities, coming after the nose, the ears and the tactile vibrissæ. It is true that in some, such as the Lagomorpha (rabbits, hares), vision is eminently useful, but the retina is still simple in structure and the eyes are probably used largely for the avoidance of relatively near objects; deprived of them, however, the animal becomes immobile. In the Sciuridæ (squirrels and particularly marmots), however, the eye with its cone-rich or cone-pure retina, becomes for the first time a dominating organ. Among the Ungulates, also, the eye becomes structurally elaborate and vision more important, although the perception of movement would appear to be biologically more useful to them than that of form; among the Carnivores, it is equally so although much reliance is placed on the other senses. The hearing of the dog is said to be up to 16 times more acute than that of man, his ability to locate sound twice as accurate, and his analysis of tone is good; but he can recognize his master visually only at the relatively short distance of some 500 metres, while a rabbit excites no attention if it does not move; normal recognition is essentially by smell. The cat has a less acute sense of smell, but it also does not see a stationary man at a distance of 12 metres, while its vision in the dark, although better than that of man, is not all-dominating, for deprived of its tactile vibrissæ it walks at night with great hesitancy. The Cetaceans are poorly equipped visually and in the analysis of its environment the whale probably relies mainly on the excellent development of its tympanic bullæ for the detection of vibratory stimuli. Apart from the squirrels it is only when the Primates and particularly man are reached that vision again dominates conduct

¹ The agility displayed by bats in avoiding obstacles at night, such as strings stretched across a dark room, has given the impression of an astonishing acuity in night vision. This feat, however, is due to hearing. Bats in flight emit a series of supersonic squeaks (with vibrations up to 50,000 per sec.), inaudible to man, as frequently as 100 times a second or more; the hearing of the echos from obstructing objects probably provides their essential means of guidance. Bats with their muzzles covered or their ears plugged cannot avoid collision.

as it does in Birds ; and with eyes of relatively simple construction as befits their direct descent from primitive Insectivores, the excellence of their visual performance depends more on the development of the central nervous mechanism of coordination and apperception than upon the end-organ itself.

It is significant that only among the anthropoid apes does there exist the ability of actively exploring the potentialities of vision in an experimental fashion. The chimpanzee, for example, will amuse himself by looking at the world in different ways—by standing upside-down, by bending down and looking through his legs, by punching a hole in a leaf and peering through it, or by making a pool of urine and regarding his reflection therein. Vision has become elevated from the reflex level of biological usefulness to that of æstheticism.

THE PERCEPTION OF LIGHT

THE LIGHT SENSE, *by which light is perceived as such and gradations in its intensity appreciated*, is the most fundamental of the visual senses, a direct development of the crude phototropic activity of the lower invertebrate organisms ; in many Vertebrates it is highly developed, more, indeed, than in man. The attainment of a high standard of sensitivity involves certain structural specializations in the eye which in their purest form are mutually exclusive of excellence of colour and form vision ; the eyes of those animals, therefore, to which an acute perception of light is a biological necessity can be differentiated from those which find greater use in keen visual acuity. This differentiation is of fundamental importance in the understanding of the visual function of Vertebrates.

From this point of view, Vertebrates can be divided into three main classes ; at each of two extremes there is a high degree of ocular specialization and a consequent loss in plasticity, and between the extremes a combination of both faculties is attained by modifications which, while lacking the efficiency of the specialized organ found at either end of the scale, ensure sufficient plasticity to allow a considerable degree of adaptability to most conditions.

(1) DIURNAL ANIMALS, the eyes of which are primarily adapted to bright light. A high degree of diurnality is seen in the passerine birds which rise and go to bed with the sun ; an extreme degree in the turtle or the marmot, an animal which never comes out by night. These are essentially visual animals in the sense that their activities are dominated by their eyes ; living in an environment flooded with light, the perception of minute amounts or fine differences of illumination is comparatively unimportant, and vision is used for the appreciation of form and perhaps colour.

(2) NOCTURNAL ANIMALS, the eyes of which are adapted to the near-darkness of night. In the less extreme degrees, a CREPUSCULAR ANIMAL finds its optimum environment in the twilight of morning or

evening. Such animals depend essentially on senses other than vision in their activities ; form vision need only be crude for merely a hazy outline is visible, and colour vision would appear to be useless.

(3) ARHYTHMIC ANIMALS, the eyes of which have sufficient plasticity to adapt themselves either to bright or dim illumination.

It can be assumed that diurnality was the primitive state in Vertebrates which presumably evolved initially in shallow waters. Nocturnality has probably been developed for two reasons—to escape from danger and to obtain food. It is likely that a lightless habitat was first sought as a refuge from stronger and more powerful enemies, whether it be the abyss of the seas, the recesses of a cave, the shelter of a stone or a burrow in the earth, or merely the protection afforded by the darkness of night. When in the early Cenozoic age the littoral or pelagic seas became increasingly populated by larger and still larger predators, in order to survive more and more of the defenceless type of fishes sought refuge in the deeper and darker depths where light becomes gradually dimmer and is ultimately extinguished ; to adapt itself to this environment the eye became more and more specialized to pick up the small amount of light available and vision necessarily became more crude. As always happens, however, the security of these refugees would not last, for predators would follow in increasing numbers from the highly populated pelagic zone to feast with less competition on the untouched store of food available in the darker waters. Thus the primitive Cyclostomes are diurnal (except *Geotria*) ; the Selachians, the Chondrosteans, the Dipnoans and the Coelacanth have all become nocturnal ; but the more highly developed Holosteans are diurnal and the eminently specialized Teleosteans which have succeeded in establishing themselves as over-all masters of the seas are of various habits as if to suit their convenience, and some of them, such as the belligerent pike, are highly diurnal.

Similarly, although the first venturers on land must have had a safe and easy time in their new environment rich in vegetable and insect food and relatively empty of powerful enemies, the evolution of more specialized types with a more efficient armature and more active habits forced many of the primitive species to seek lightless surroundings or the cover of night in order to survive ; the penalty for failure in this adaptation was usually extinction. Apart from the frogs, all Amphibians which have survived are therefore markedly nocturnal or secretive in habit ; apart from the turtles, all Reptiles which have survived are also nocturnal except the majority of the recently developed lizards and their off-shoot, the still more modern snakes, many of which, initially nocturnal and burrowing, have acquired a new diurnality. Freed from the danger of land animals in their new aerial environment, most Birds can afford to be diurnal, although

in their search for food many have become crepuscular and a few, particularly the owls, essentially nocturnal.

Flightless birds are therefore in a peculiarly precarious position and many of them have been exterminated: the moas in New Zealand on the arrival of man (Fig. 737); the dodo of Mauritius on the arrival of mammals (Fig. 738); while the kiwi of New Zealand, even although taking refuge in nocturnality, is now almost extinct (Fig. 739).

Similarly in their search for safety from the larger Amphibians and Reptiles which inhabited the earth at the time of their emergence, the early Mammals were nocturnal or crepuscular—all the Monotremes, all the smaller and more primitive Marsupials and most of the primitive Placentals. Among these last, only a few have acquired



Primitive
Amphibian



Primitive
Reptile



FIG. 737.—THE MOA.



FIG. 738.—THE DODO.



FIG. 739.—THE KIWI.



Primitive
Mammal



Tupaia



Castor

diurnality, particularly the tree-shrews (*Tupaia*) among the Insectivores, and the squirrels (except the flying squirrels) among the Rodents; to these the diurnal habit was possible owing to the relative safety of their arboreal life and its acquirement was probably stimulated by the necessity for constant agility in their environment. The other diurnal Rodents are few—the beaver, *Castor*, the cavy, *Dolichotis*, and the pika, *Ochotona*; the coney, *Procavia*, is of the same habit. The small Carnivores, except the viverrid, *Cynictis*, and the suricate, *Suricata*, are also primarily nocturnal or crepuscular, but the larger Marsupials and the Ungulates and the larger Carnivores have become arhythmic, the first two emerging into the daylight because of the safety provided by their agility and fleetness, the last because of their ferocity and the excellence of their weapons of offence. As did their ancestors, the Insectivores, the early Primates found safety in nocturnality; practically all the Prosimians are nocturnal except some members of the family of lemurs,¹ but having acquired safety in their agility and intelligence, all the Simians except the night-monkey *Nyctipithecus*, are diurnal or arhythmic.

¹ A few species are diurnal such as *Propithecus*, *Indris*, and *Hapalemur*.

We have noted that the ocular characteristics of a nocturnal and a diurnal eye are essentially incompatible ; in the arhythmic eye a compromise is reached. The nocturnal eye is attuned to a high development of the light-sense ; in the diurnal eye this gives place to the

FIGS. 740 TO 749.—NOCTURNAL, DIURNAL AND ARHYTHMIC TYPES OF EYE.
(In each case the lens is unshaded.) The eyes are not drawn to scale.

Note the huge size of the lens and its set-back position in fully nocturnal types (Figs. 740-3), and its small size and anterior position in fully diurnal types (Figs. 747-9).

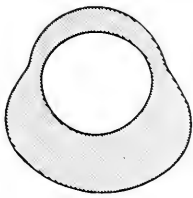


FIG. 740.—A nocturnal gecko.

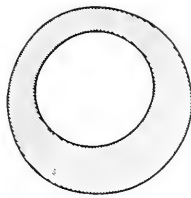


FIG. 741.—A rat.



FIG. 742.—An opossum.

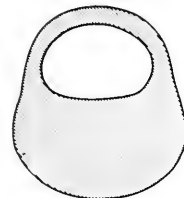


FIG. 743.—A lemur.

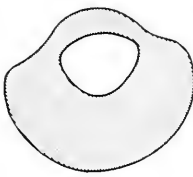


FIG. 744.—A diurnal gecko.

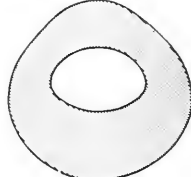


FIG. 745.—A lynx.



FIG. 746.—An owl.



FIG. 747.—The chameleon.

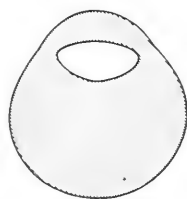


FIG. 748.—A chimpanzee.



FIG. 749.—A pigeon.

apparatus required for keen visual acuity. In order to attain efficiency *a nocturnal eye evokes special peculiarities* both in its optical system and in the organization of the retina.

I. *The optical system* demands a large eye to gather as much light as possible, a widely dilated pupil to allow the maximum amount of light to enter, and a large spherical lens set far back from the cornea to place the optical centre near the retina so that light transmitted

through the dioptric system is concentrated into a small image of the maximum possible brightness (Figs. 740 to 743 : 752 to 754).

Enlargement of the eye in the interests of nocturnal vision is common but is seen in its most extreme degree in certain deep-sea Fishes wherein the eyes may be larger than the remainder of the head ; this tendency, in combination with the evolution of a maximal size of the lens, leads to the development of a tubular eye when the head is not sufficiently big to accommodate a spherical organ of the necessary dimensions.¹ The large lens occupying a high proportion of the globe and closely approaching the retina is well seen in the eyes of the smaller bats and Rodents (Figs. 741).²

FIGS. 750 AND 751.—THE EYES OF BIRDS.

To contrast the relatively small eyes of a diurnal bird and the large eyes and widely open pupil of a nocturnal bird.



FIG. 750.—The crowned hawk eagle, *Stephanoaetus*.



FIG. 751.—Savigny's eagle owl, *Bubo ascalaphus*.

A TAPETUM LUCIDUM is an accessory to the optical system to aid vision in dim illumination ; it is essentially a mirror-arrangement so that light, having traversed the sentient elements of the retina, is reflected backwards again and its effective intensity is thus augmented.³ Not only is the amount of light available for stimulation thus materially increased but slight differences in luminosity between an object and its background are proportionately accentuated so that the total effectivity of vision in dim illumination is correspondingly improved. It is this reflected light seen by an observer standing beyond the

¹ p. 322.

² It is to be remembered that, for entirely different reasons spherical lenses are also found in aquatic Vertebrates (except Sirenia)—Cyclostomes, practically all Fishes (except amphibious types, as *Periophthalmus*), aquatic amphibians, marine turtles and Crocodilians, and Cetaceans and Pinnipeds. See p. 277.

³ The effective intensity would theoretically be doubled by a perfect mirror. A tapetum probably ensures an increase of about half as much—40% in the cat (Weale, 1953).

FIGS. 752 TO 755.—THE EYES OF PLACENTALS.

To contrast the large prominent eyes of nocturnal Placentals (Figs. 752-4) with the relatively small eyes of an arhythmic Placental (Fig. 755) (Zool. Soc., London).



FIG. 752.—The fruit bat, *Pteropus*.



FIG. 753.—The two-toed sloth, *Choloepus*.



FIG. 754.—The potto, *Perodicticus potto*.



FIG. 755.—The langur, *Pithecus nemaeus*.

animal's near-point (10 to 20 feet in emmetropic animals with little accommodation) which gives rise to the striking "eye-shine" in suitable optical conditions so familiar in the cat family.¹ The peculiar hue often associated with a beautiful iridescent effect is due to interference phenomena depending on the size and stratification of the reflective elements of the tapetum and irregularities on its surface (Brücke, 1845 ; Hess, 1912 ; Roggenbau, 1928), an effect which may perhaps be heightened by fluorescence (Hosoya, 1929).²

To be effective in this way the tapetum must lie behind the receptor elements. Two sites have been utilized, either the pigmentary epithelium of the retina or the choroid, and in both cases the pigment normally found in the former must be eliminated or reduced to insignificant proportions to allow the light to traverse it. Both the utilization of diffusely reflected light and the elimination of pigment, of course, militate against acuity of vision in bright illumination ; it is, therefore, interesting and significant that although a tapetum frequently occurs with an area centralis, it is never found in an eye with a true fovea. Whereas in the purely nocturnal eye a static tapetum is thus an effective visual aid, an oclusable tapetum wherein the mirror can be used in dim light and obscured in bright light is a much more efficient and plastic mechanism for the arhythmic eye.³

(i) RETINAL TAPETA. The pigmentary epithelium of the retina is converted into a mirror by a packing of the cells of this layer with guanine (in Teleosts and Crocodilians) or some related substance (in Mammals). Guanine is a purine related to uric acid and, either in the pure form or as the calcium salt, is deposited as highly reflecting crystals. We have already studied its effect as a silver-coated mirror in the scales of fishes in determining the colour of their integument ; deposited in the retinal epithelium a similar reflection of incident light is attained. In a tapetum of the static (non-occludible) type the epithelial cells are filled with reflecting crystals and the fuscine is reduced to a minimal amount. Such a tapetum is rare, being found among some abyssal Teleosts (*Evermanella*, etc.), in Crocodilians, and, among Mammals, in the larger bats (*Megachiroptera*) (Fig. 581) and (occupying the entire upper half of the fundus) in the Virginian opossum, *Didelphys virginiana*. Some reflecting crystals are also seen in the retinal pigmentary epithelium of the dog which probably aid the reflection of light by the underlying choroidal tapetum.



Didelphys

(ii) CHOROIDAL TAPETA (of the non-occludible type) may be of three types :

¹ For this reason the ancient Egyptians worshipped the cat, the eyes of which magically reflected the light of the Sun-god even at night.

² Cf., the diffractive coloration of the integument, p. 89.

³ p. 612.

- (a) a GUANINE TAPETUM in certain fishes—Chondrosteans, the coelacanth and certain bathypelagic Teleosts—wherein compact layers of cells are packed with guanine crystals ;
- (b) a TAPETUM CELLULOSUM (Fig. 580), a closely packed series of layers of endothelial cells filled with doubly refractive (? lipoid) rodlets, found in a relatively small area of the upper half of the fundus of all Carnivores except *Cynictis* and *Suricata*, over the entire posterior part of the fundus of Pinnipedes, and in the nocturnal lemuroids ;
- and (c) a TAPETUM FIBROSUM (Fig. 579), formed by a tendon-like condensation of fibrous tissue. This last has a relatively widespread distribution—in many pelagic Teleosts, in certain Marsupials (the dasyure, *Dasyurus*, the Marsupial wolf, *Thylacinus*, the Tasmanian devil, *Sarcophilus*, and the flying phalanger, *Petaurus*), among the Rodents in two species (the spotted cavy, *Cuniculus*, and the flying squirrel, *Pteromys*), in all Ungulates (except the Suoidea and Tylopoda), in the elephant, the Cetaceans, and in the only nocturnal Simian, the night-monkey, *Nyctipithecus*, in which the eye-shine from the tapetum is unusually brilliant.

*Suricata**Sarcophilus*

II. *The organization of the retina* of the nocturnal eye depends essentially on two features—great sensitivity of the sentient elements and a high degree of summation within the retinal structure so that a large number of receptor elements can combine to stimulate a single optic nerve fibre (Figs. 756, 757). It has generally been accepted that the rods were particularly sensitive to light, a property which was considered due to the great sensitivity of rhodopsin or the closely related pigments with which they are provided. It may be that this assumption is incorrect, for the evidence now available points to the possibility that the rods and cones, *considered individually*, are equally sensitive to light and that the apparent superiority of the rods in this respect may be entirely due to summation by which a ganglion cell can be excited into activity by a comparatively large number of stimuli each of which acting by itself would be subliminal. In the present state of our knowledge it would be dangerous to dogmatize on this problem ; it has most recently been discussed by Weale (1958).

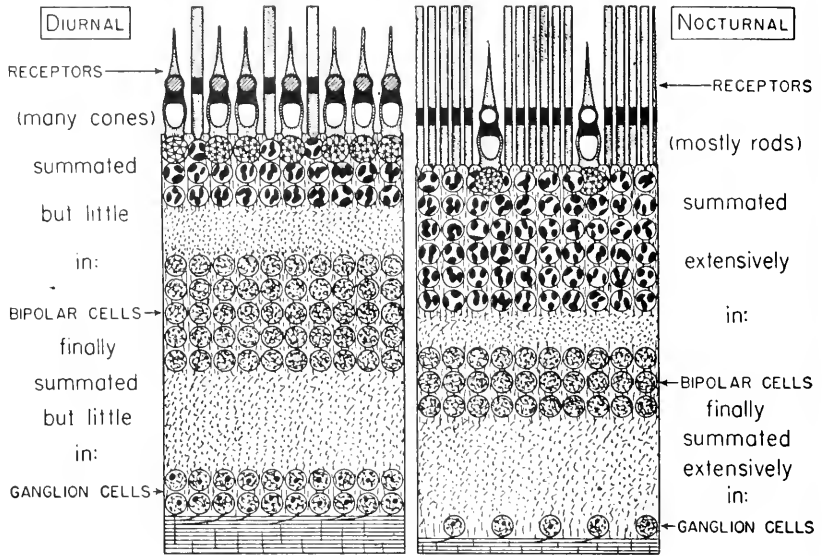
However that may be, the rods, either by reason of their own properties or on account of their neural connections, are specifically adapted to a high degree of sensitivity and therefore subserve scotopic vision, while the cones are adapted to a high degree of analytical acuity and therefore subserve photopic vision ; these structures are therefore differentiated sharply from the functional point of view. Their structural differentiation, however, is not always easy since



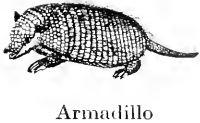
intermediate types exist¹; in general it may be said that in most vertebrate types the retina is duplex, but in nocturnal species the retina becomes rod-rich or pure-rod with a corresponding reduction or elimination of cones.

A PURE-ROD RETINA is seen only in a few entirely nocturnal animals²—the Selachians (except a few species, *e.g.*, the ray, *Myliobatis*, the dogfishes, *Mustelus* and *Squatina*); a few deep-sea Teleosteans; among the Reptiles, some nocturnal

FIGS. 756 AND 757.—RETINÆ OF DIURNAL AND NOCTURNAL ANIMALS.



The diagrams represent two related species, one of which is diurnal and the other nocturnal. The different ratios of visual-cell types call for different relative numbers of the various conductive-cell types, leading to varying degrees of summation in the optic nerve fibres and producing characteristic differences in the relative thickness of the retinal layers (Gordon Walls).



lizards (nocturnal geckos) and snakes (some nocturnal colubrids as *Hypsiglena* and *Phyllorhynchus*); the Monotreme, echidna; the armadillo, *Dasypus*; and the bats (Chiroptera). It is presumed without clear histological proof to occur in a few other types—in the Chimæras, in *Lepidosiren* among the lung-fishes, in the Caecilians among Amphibians, and in a few Mammals such as the hedgehog, the shrew, ? in the chinchilla, in the seals (Phocidae), the whales (Cetacea), the nocturnal lemuroids, *Tarsius*, and the night-monkey, *Nyctipithecus*.

A ROD-RICH RETINA with a few cones occurs in certain Teleosteans such as the burbot, *Lota* (810,000 rods and 3,400 cones per sq. mm., Wunder, 1925), in the eelacanth, in *Sphenodon*, and in some nocturnal Rodents (*Rattus*, *Mus*, *Cavia*, etc., in which the proportion of rods to cones is about 100 : 1).

¹ p. 251.

² p. 603.

So far as the rods themselves are concerned, sensitivity is further increased by several expedients all of which tend to lower their threshold by increasing the amount of rhodopsin available in a given area. Close packing of the individual elements with this end in view is seen carried to its greatest lengths in certain deep-sea Selachians (*Etmopterus*, etc.) and Chimæras, while the concentration of visual cells in a pure-rod or rod-rich area centralis probably serves a similar purpose.¹ To increase the amount of available visual purple still further, the outer segments of the rods may be lengthened to a remarkable extent as is again seen in certain bathypelagic Teleosts (*Lampanyctus*, *Argyrolepecus*, Verrier, 1935; Contino, 1939); the rods may be arranged in layers one above the other (3 in the peripheral retina, 6 in the fovea in *Bathylagus*); while these elements may become massive and thickened as occurs in Amphibians and some nocturnal geckos (Fig. 433).

The degree of *summation in the retina* is the principal expedient employed to increase sensitivity whereby large numbers of visual cells converge upon a single bipolar cell, and several bipolar cells themselves converge upon a single ganglion cell and optic nerve fibre so that a meagre stimulus applied to each of a large number of visual receptors can be summated to produce one nerve impulse. In the organization of the retina summation is a characteristic of the rods. In Osterberg's (1935) counting, there are 110,000,000 to 125,000,000 rods and 6,300,000 to 6,800,000 cones in the human retina associated with about 1,000,000 optic nerve fibres, that is, an overall summation of the order of 125 : 1. In the retinae of nocturnal types it is not uncommon for many more receptors to be summated to a single ganglion cell.

An additional summation may occur more proximally in the visual pathway : thus in the higher Primates there is a one-to-one relationship between the terminals of the optic nerve fibres and the cells in the geniculate body, but in the cat, which has a high degree of sensitivity to light, it would appear that 30 to 40 optic nerve terminals are related to each geniculate cell (Glees, 1941-42).

The characteristics of a diurnal eye attuned to a high visual acuity are, as we shall see,² almost precisely the opposite of those of a nocturnal eye (Fig. 747) : a forward location of the optic centre so that a large retinal image is formed to allow the resolution of detail, an adequate pupillary stop to eliminate aberrations, and a cone-rich retina with a low summation to the ganglion cells so that the retinal image can be accurately analysed.

In the most exclusively diurnal types the retina may contain cones only : such a PURE-CONE RETINA is found among Dipnoi in *Neoceratodus* ; among the Polypterini in *Calamoichthys* ; in most diurnal lizards ; in diurnal colubrid



Calamoichthys

¹ p. 657.

² p. 637.

snakes ; and in diurnal Sciuridae, particularly the marmot. A practically pure-cone retina is found in Chelonians.

The characteristics of an arhythmic eye are necessarily a compromise between the first two types, but several expedients are available to protect an eye adapted to scotopic vision from excessive light. A purely diurnal eye (such as that of most Birds or some lizards and snakes with pure-cone retinae) is completely incapacitated in dim illumination, but an eye that is essentially nocturnal can be made into a useful organ in the brightest daylight. These expedients are both optical and retinal in nature.



Dasyurus



Hyæna



Basking shark



Coney

(a) A markedly CONTRACTILE PUPIL is the simplest and most common optical device. With this simple expedient alone a nocturnal animal may be rendered arhythmic. From the structural point of view, the easiest plan is contraction to a stenopœic slit as is commonly seen in some selachian Fishes, many Reptiles (*Sphenodon*, Crocodilians, many lizards and nocturnal snakes) in some Marsupials (*Dasyurus*, *Trichosurus*), the dormouse, *Glis*, the small Carnivores (such as the cat), Pinnipedes, the hyænas, and most Prosimians (Figs. 758-9). Such a slit-pupil, if the aperture is sufficiently narrow, will allow an essentially nocturnal animal to hunt effectively in bright daylight (the nocturnal geckos or the cat) or to bask in comfort in the sun (the crocodile, a nocturnal snake or a basking shark). Only a few species have a sufficiently powerful sphincter to effect the mechanically more difficult feat of contracting a round pupil to a stenopœic pin-hole—the teleostean pearl-fish, *Encheliophis* ; sea-snakes (Hydrophinae) ; the two-toed sloth, *Choloepus* ; the African jumping hare, *Pedetes* ; and, above all, the Prosimians, particularly *Tarsius*, the large round pupil of which contracts to a pin-hole 0.5 mm. in diameter (Fig. 760). Other similar expedients are less common and include the expansible OPERCULUM associated with the pupil of many skates and rays, teleostean flat-fishes and Cetaceans, the UMBRACULUM of the coneys (Hyracoidea), or the parasol provided by the CORPORA NIGRA of the Ungulates.¹

(b) An OCCLUSIBLE TAPETUM is a second expedient adopted by certain Fishes to achieve some degree of arhythmicity ; in dim light the reflecting surface is exposed in which case the tapetum acts as in a nocturnal eye, but in bright light it is covered with migrating pigment so that in these circumstances the animal is not dazzled. Such a structure is seen in the elaborate choroidal tapetum of Selachians in which the mirror-like guanine plates can be covered when necessary by the migration of the melanin in the choroidal chromatophores (Fig. 300),² and the retinal tapetum of certain Teleosts of the minnow (Cyprinidae) and perch (Percidae) families³ wherein the guanine crystals in the inner halves and processes of the cells of the pigmentary

¹ p. 649.

² p. 283.

³ p. 305.

FIGS. 758 TO 760.—THE CONTRACTILE PUPILS OF PLACENTALS.



FIG. 758.



FIG. 759.

FIGS. 758 AND 759.—The pupils of the cat in dilatation (Fig. 758) and in contraction showing the extremely narrow vertical slits (Fig. 759).

FIG. 760.—The tarsier, *Tarsius*, to show the pupils in contraction ; they are horizontal slits but practically circular (photograph by Douglas Fisher).

epithelium can be swamped and obscured by the migration of fuscine from the outer halves of the cells.

(c) Adaptation both to scotopic and photopic vision is also to a considerable extent facilitated both by dynamic changes in the retina and in its static organization. Into the first category come the RETINAL PHOTO-MECHANICAL CHANGES, more marked in the lower Vertebrates than in the higher. These comprise a migration of the fuscine from the bodies of the cells of the pigmentary epithelium into their processes which dip inwards between the rods and cones thus enveloping them in a dark sheath of pigment in bright illumination, and its return back to the cell-bodies in dim illumination so that the visual elements are freely exposed to any light there may be available (Figs. 761 to 764). A corresponding movement may involve the visual cells themselves, the myoid element of which is sometimes strongly contractile.¹ The rods are usually relatively static and in the few species wherein they migrate they elongate towards the pigment of the epithelial cells to take refuge from bright light. The cones, on the other hand, may remain stationary or contract inwards, away from the pigmentary processes.

The migration of the pigment was first noted in the frog by Czerny (1867), Boll (1877) and Angelucci (1878), and was exhaustively studied by Kühne (1878), Engelmann (1855), v. Hess (1910), and a host of others (see Arey, 1916); in *Rana temporaria* the migration occurs even in the excised eye, a reaction which demonstrates that a local control exists (Weale, 1956). In other species of Anurans (*Xenopus*) no demonstrable migration of pigment occurs (Saxén, 1953; Weale, 1956). The movement, however, is relatively slow, being fully evident within half a minute but is not complete for 50 minutes, while its return in darkness is slower still (1 to 2 hours, Arey, 1916). Migration is most evident in the lower Vertebrates; it is absent in Selachians for in the greater part of their retina there is no pigment, but is marked and extensive in many Teleosteans, less extensive and somewhat slower in Anurans, still less and slower in Urodeles, slight and slow in most Reptiles (turtles, Crocodilians, and less in lizards), more marked and rapid in Birds, but has never been adequately demonstrated in Mammals although in this class the retina has been said to cling more tenaciously to the pigment epithelium after illumination (see v. Hess, 1912; Detwiler, 1916-23; Laurens and Detwiler, 1921; Holm, 1922; Bayliss *et al.*, 1936).

The migration of the rods and cones on illumination is more rare and less dramatic, but takes place more rapidly (about 2 minutes) and with less intensities of illumination than the migration of pigment (Arey, 1919); these movements are said to be associated with swelling on illumination and subsequent shrinkage of the rod and cone nuclei (Puff, 1951-53). It is most marked in *Amia* and teleostean Fishes (apart from the flat-fishes), but the eel, *Anguilla*, is unique in that only the rods participate in the movement. Among Teleosteans these movements have received a considerable amount of study.² The rods retract and the cones elongate to enter the guanine layer of the retinal tapetum in dark adaptation (the pike-perch, *Lucioperca*—Wunder, 1930; the guppy, *Lebistes*—



Xenopus



Amia



Anguilla

¹ Such movements may occur in Invertebrates, cf., *Notonecta*, p. 170.

² For the diurnal variation in the migration of visual cells, see p. 19.

FIGS. 761 TO 764.—PHOTO-MECHANICAL MOVEMENTS (Katharine Tansley).

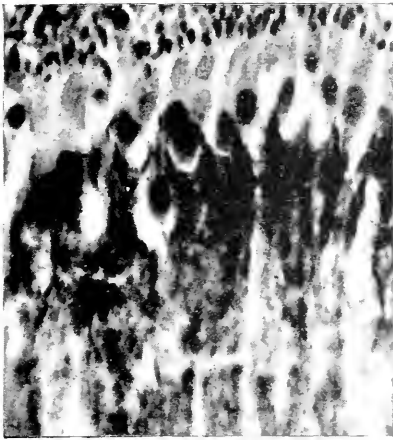


FIG. 761.

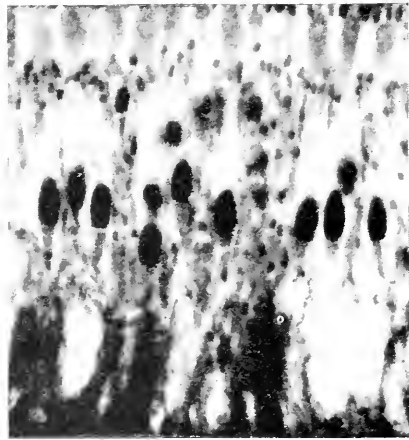


FIG. 762.

FIGS. 761 AND 762.—Pigmentary migration in a fish (the bleak *Alburnus lucidus*).

FIG. 761.—The changes in light adaptation. The rods have moved outwards and the cones inwards; while the pigment has moved inwards to shield the rods and envelop the outer limbs of the cones.

FIG. 762.—The changes in dark adaptation. The cones have moved outwards and the rods inwards; while the pigment has migrated outwards to expose the rods.

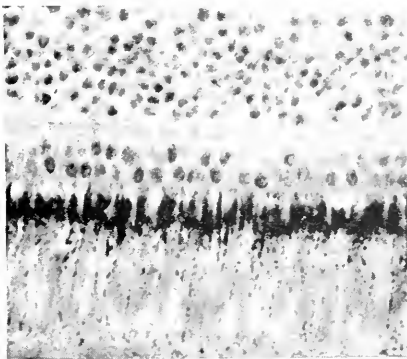


FIG. 763.

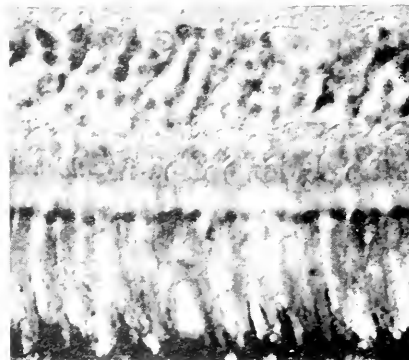


FIG. 764.

FIGS. 763 AND 764.—Pigmentary migration in the frog, *Rana temporaria*.

FIG. 763.—The retina in light adaptation. The pigment has migrated inwards to shield the rods.

FIG. 764.—The retina in dark adaptation. The pigment has moved outwards to expose the rods.

*Fundulus**Ameiurus*

H. Müller, 1954 ; and others) ; the excursions are often considerable, the rods, for example, of the killifish, *Fundulus*, and the catfish, *Ameiurus*, changing from a length of 90–100 μ in light adaptation to 30–35 μ in the dark-adapted eye (Detwiler, 1943). Among Amphibians, the Anurans show a more marked degree of migration than Urodeles and in each case the cones move more rapidly and extensively than the rods. In Reptiles the phenomenon is very slight and slow, if it occurs at all ; in Birds cone migration is sometimes rapid and extensive ; and in Mammals no movements of this type have been reported except by Garten (1908) in monkeys (Angelucci, 1892 ; Garten, 1908 ; Hess, 1912 ; Detwiler, 1916 ; Laurens and Williams, 1917 ; Kohlrausch, 1918 ; Laurens and Detwiler, 1921 ; Loevenich, 1948).

The pupillary response and these retinal photo-mechanical changes are supplementary in time in so far as the former is immediate and rapid in its action while the latter is slow. It is also interesting that their efficiency shows a mutual relationship. The photo-mechanical migrations in the retina are more marked in the lower Vertebrates (apart from Selachians) ; in Fishes (apart from Selachians) pupillary movements are slow and restricted and the muscles respond autonomously to light. At the other end of the scale the nervously controlled pupil of the higher Vertebrates is so active and effective that retinal migrations have become superfluous and have disappeared.

The STATIC ORGANIZATION OF THE RETINA is of importance in arrhythmic animals. Obviously such a retina must be duplex, but to attain sensitivity the rod population must be considerably higher than that of the cones. The most effective distribution is seen in Primates wherein the cones are massed in an area centralis suitably situated to subserve form vision¹ while the rods are particularly numerous in the peripheral retina ; in such a case the central area is relatively blind in dim illumination, a circumstance of little inconvenience, however, since acuity is impossible in these circumstances in any case and light-perception is as easily served by the peripheral as by the central retina.

By the use of one or more of these expedients a very high degree of ABSOLUTE SENSITIVITY TO LIGHT can be attained. Theoretically it would be expected that the most sensitive eyes in the vertebrate phylum are to be found in bathypelagic fishes which make use of the minute available traces of light by means of a large eye with a huge pupil, a brilliant tapetum and an enormous and heavily summated rod-population. Among Selachians a typical example of such a combination is seen in the deep-sea luminous shark, *Etmopterus* ; it is also seen in the Chimæras and bathypelagic Teleosts. In some species of the latter the state of dark adaptation has become permanent, the retinal epithelium losing its pigment and photo-mechanical changes

¹ p. 656.

being eliminated. The owl may be taken as typical of nocturnal birds ; Hecht and Pirenne (1940) taking the minimal observable contraction of the pupil to green light as their criterion, reported an absolute threshold of 1.5×10^{-7} ml., their own threshold under the same conditions being 4.0×10^{-7} ml. The astonishing visual performance possible in owls in dim illumination was verified by Dice (1945-47), who found that the barn-owl can detect and pounce upon dead mice at a distance of 6 feet under an illumination of 7.3×10^{-7} f.c. It is to be remembered that clear starlight has a much higher intensity than this, of about 8×10^{-5} f.c.¹

Among arrhythmic animals, adaptations to varying luminosity may also reach a much higher efficiency than in man : it has long been traditional that the wise rider relies upon the horse to pick its own footsteps during the night. In this respect most scientific work has been devoted to the cat. In behavioural experiments involving a choice between darkness and a minimal degree of light, remarkably constant results for the absolute limits of retinal sensitivity have been found—Mead (1942), 1.3×10^{-7} ml. ; Bridgeman and Smith (1942), 8.2×10^{-8} ml. ; Gunter (1951), 9.92×10^{-8} ml., the average threshold for man being higher—of the order of 5.8×10^{-7} ml.

While the sensitivity to light in most Vertebrates is high, the more highly evolved faculty of the DISCRIMINATION OF VARIATIONS IN INTENSITY, is apparently less efficient, although in many cases the failure may be due to lack of attention in experimental conditions rather than lack of appreciation. Little conclusive work has so far been done on this problem and some of it is contradictory. v. Hess (1909) claimed that the silverside, *Atherina*, responded to white lights differing only by 1 : 1.23 in brightness ; but the carefully controlled observations of Bauer (1909) on this and other types of Teleosteans, which have since been confirmed, tend to show that they are relatively indifferent to wide variations of intensity of white light (Sgonina, 1933, on the minnow, *Phoxinus*, and others). Thus, working with the mud-fish, *Umbra*, and the stickleback, *Eucalia*. White (1919) found in training experiments that they had difficulty in making any discrimination between pigmentary greys and whites ; this she corroborated at a later date (writing under the name of Hineline, 1927). Similarly, Cora Reeves (1919) substantiated that the dace, *Scmotilus*, could not distinguish differences in intensities greater than 1 : 4 although the sun-fish, *Lepomis*, showed a better performance (1 : 2), an observation corroborated by Hurst (1953). Moreover, goldfish have been taught to choose one of three intensities, and to choose one light on the basis of its relationship with two others when the intensities as well as the

*Atherina*

Goldfish

¹ The factor to convert foot-candles into millilamberts is $\times 3.382$.



Raccoon



Polecat

positions were changed after each trial (Perkins and Wheeler, 1930 ; Perkins, 1931). Within limits, therefore, an appreciation of differences of intensity is possible to Fishes.

Similarly, in training experiments Wojtusiak (1933) found that turtles had great difficulty in distinguishing shades of grey. According to the findings of Hamilton and Coleman (1933) training experiments showed that a diurnal bird (the pigeon) is more attentive to changes in hue than in brightness ; while in most Mammals the opposite obtains. Among these, in most of the nocturnal types which have been investigated, the discrimination of brightness has been found to be excellent (Cole and Long, 1909, in the raccoon ; D. Müller, 1930, in the polecat ; Munn, 1932, in the rat) ; in the guinea-pig, however, Sgonina (1936) found that the intensity of two greys had to differ by $1/3$ before differentiation of them could be made. Among diurnal types Sälzle (1936) found that the discrimination of brightness was poor. In arhythmic types, on the other hand, it may be very good indeed. Thus Orbeli (1909), eliciting conditioned reflexes in salivary secretion in the dog, found that this animal was capable of differentiating perfectly between closely related shades of grey (e.g., between 49 and 50 of the Zimmermann scale) which are quite indistinguishable to the human eye, whether they were presented successively or simultaneously. Indeed, so far as the dog is concerned, Pavlov (1911-27) concluded that the analysis of the intensity of illumination is so highly developed that a human experimenter is unable to determine its limits.

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THE PERCEPTION OF COLOUR

We have already seen that among Invertebrates the phototactic reactions of some Crustaceans vary with the wave-length of the stimulating light and that colour vision on the perceptual level has been demonstrated in some Insects; in the vertebrate phylum its undoubted occurrence as a significant factor in behaviour has been substantiated in only a few classes—teleostean Fishes, a few Reptiles, Birds and the higher Primates. The subject, however, raises many intriguing questions. So far as the evidence goes, the eyes of all vertebrates including man are stimulated by approximately the same range of the spectrum (760 $m\mu$ –390 $m\mu$) with the highest sensitivity at a band with a wave-length varying between 500 and 550 $m\mu$; it is no coincidence that this corresponds roughly with the transmission spectrum of water. The visual mechanism of Vertebrates was first evolved in water and their photo-pigments were presumably developed as sensitizers to allow their possessors to leave the brightly-lit surface and penetrate more deeply into the darker depths of the sea; and it would be surprising if their descendants discarded a mechanism which their ancestors had found of such value. It is true that Hamilton and Coleman (1933) demonstrated in the homing pigeon a capacity of hue-discrimination slightly beyond the limits of human perception, a faculty which may apply to the stickleback, *Gasterosteus*, in the ultra-violet region of the spectrum (Merker, 1934–39); but in general, so

far as is known, the spectral limits of the vision of all Vertebrates are approximately the same, and include nothing corresponding to the visibility of the ultra-violet to insects.¹

Within this spectral range the human eye can differentiate many hues, qualities independent of the luminosity ; and to man, colour sensations are highly overlaid with æsthetic values. These, however, must take a subsidiary place in vertebrate evolution ; in the animal hue-discrimination is never developed to a corresponding extent and although in certain species it may have a secondary biological value in sexual displays or as a means of concealment and advertisement, it would appear to be essentially a mechanism designed to increase the visual acuity by acting as an adjuvant to the discrimination of brightness. Evolved out of the light-sense with a view to obtaining a more critical analysis than could be provided by the appreciation of differences in luminosity alone, there is no legitimate reason to assume that different bands of the spectrum excite in animals the perceptual experiences recognized as colour by us. Moreover, as would be expected from its biological purpose, hue-discrimination is found largely in intensely visual Vertebrates with highly diurnal activities and provided with a cone-rich retina, a fovea and an effective accommodative apparatus ; a colour sense, in fact, is associated with good visual acuity, and that we shall see presently ² is rare among Vertebrates. When vision is vague and limited largely to an appreciation of luminosity and movement, the refined discrimination provided by colour vision is likely to be of little importance ; and to the nocturnal animal such a faculty would seem to be meaningless.

The investigation of colour vision in animals has excited much attention since the early work of Graber (1884-85) on fish. Even in human experiments this is a notoriously difficult subject, but in animals the difficulties increase manyfold ; unless the stimulus is presented with the utmost care it is difficult to exclude variants other than hue-discrimination, such as changes in luminosity, in any choice the animal may make. Moreover, the tractability, responsiveness and intelligence required to produce a consistent response are frequently lacking so that in many cases a lack of a colour sense may be presumed when conduct may have been determined by irritability, untrainability or brainlessness. If, for example, a colour sense is not highly developed and does not play a prominent part in the everyday behaviour of the animal, experimental testing will probably involve difficult discriminations comparable to a complicated intelligence test in man in which the subject, unable to grasp completely the point at issue, has to rely on

¹ Owls have been credited with vision in the infra-red, but this is not the case—see p. 630.

² p. 637.

guesses which may often be misleading and are rarely consistent.¹ Because this limitation has not been realized, much of the work on this subject has been scientifically worthless and in the literature many contradictions are to be found.

The methods employed in the exploration of the colour vision of animals embrace the two classes we have already discussed as being available for the analysis of other visual functions ²—objective and subjective.

THE OBJECTIVE METHODS OF APPROACH depend on the observation of a measurable physical phenomenon presumed to be determined by a specificity in the retinal response to different wave-lengths ; they suffer from the weakness that such a differential response does not necessarily imply a conscious appreciation of hue. The luminosity curve for the dark-adapted human eye, for example, shows a differential sensitivity to different wave-lengths and yet does not imply a sensation of colour. Even although more than one retinal mechanism may be stimulated and a physical basis may be shown to exist where-upon colour vision could be based, vision on the perceptual level may nevertheless be achromatic. Indeed, as Pumphrey (1949) suggested, it may well be that most animals with highly developed eyes have the fundamental mechanism for mediating colour vision, but it is utilized only by the few to which it is a biologically useful attribute.

Several such phenomena have been utilized :

(a) *Dermal colour changes.* One of the earliest arguments employed in ascribing the faculty of colour vision to animals was the occurrence of changes in colour in the integument or its appendages in response to the environment,³ a study which was first applied on a scientific basis by Karl von Frisch (1912) to fishes ; it seems unlikely that Nature would evolve a complicated method of camouflage based on colour if differences in hue were not appreciated by the enemies it was advisable to avoid, while the assumption of brilliant colours as a method of sexual attraction becomes meaningless if the potential mate is unresponsive to the stimulus so elaborately provided. This is true ; but it is to be remembered that many of the colour changes designed to mimic an environment are reflex⁴ and need not enter into consciousness, and even if they are it is conceivable that in some cases the changes appreciated by us as hue may be interpreted by some animals in terms of luminosity, providing changes in contrast rather than in quality. This approach is therefore suggestive, particularly in the case of teleostean Fishes and Birds, but cannot be accepted as implying rigid and incontrovertible proof of the existence of true colour vision. Moreover, if it is used at all, the method must be employed only on adequately controlled experimental trials.

(b) *The pupillary reactions.* Observations of the differential effect of wave-bands in the spectrum in the induction of pupillary contractions stem from the original observation of Sachs (1892-1900) that with lights of equal energy this

¹ See Smith (1912).

² p. 568.

³ p. 82.

⁴ p. 92.

reaction varies directly with the luminosity of the coloured light employed. Sachs in this way verified the occurrence of a Purkinje shift in the pupillomotor activity of the human eye, finding a maximal reaction in the yellow in light-adaptation, in the blue-green in dark-adaptation¹; in totally colour-blind subjects (rod-monochromats) the reaction typical of dark-adaptation is obtained (Fig. 765). This technique was first applied by Abelsdorff (1907) to Birds and later and on a much larger scale to Fishes and a host of other animals by v. Hess (1907-22) and others. In some cases the method probably gives an assessment

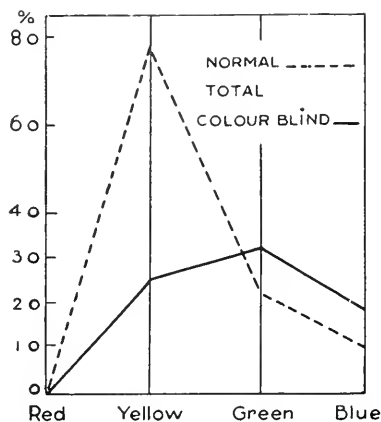


FIG. 765.—THE PUPILMOTOR REACTION.

The relative pupillomotor values of coloured light in the normal (light-adapted) eye and in the totally colour-blind (after Engelking).

of the spectral range and relative luminosity of the wave-lengths which stimulate the retina, but its interpretation in terms of colour vision is quite illegitimate. Abelsdorff, for example, showed that the pupil of the (diurnal) pigeon, or (arhythmic) dog was less responsive to green and blue, and that of the (nocturnal) owl or cat more responsive to the blue than the human pupil. v. Hess, however, went much further and argued that if the maximal pupillary contraction were in the yellow, the eye was photopic in type and colour vision was present, if in the green that it was absent; if the process of adaptation were accompanied by a decreased sensitivity for the red end of the spectrum and an increased sensitivity for the blue, colour vision was presumed to exist. That this conclusion is illogical is obvious, since it begs the questions that the luminosity curves of animals are the same as in man, that the presence of a duplex retinal mechanism as indicated by

(c) *Electro-retinographic responses* have been applied to the study of colour vision in animals since the demonstration by Himstedt and Nagel (1902) that the retinal action-currents of the frog showed a Purkinje shift, the peaks of maximum sensitivity being the same as in the human retina—560 m μ in the light-adapted and 507 m μ in the dark-adapted eye. In further elaboration of this work, Granit and his co-workers (1935-47) found that there were at least three systems in the frog's retina reacting selectively to light of different wave-lengths. Similarly in Birds, Piper (1905) found that a maximal sensitivity to monochromatic lights in diurnal types (fowl, etc.) was at 600 m μ , while that of nocturnal birds (owl) was at 535 m μ . A similar Purkinje shift has been recorded in the eyes of Fishes (carp, tench, etc.) and Mammals (cat) with a duplex retina, but not in those such as the tortoise with a (?) pure-cone retina, nor in nocturnal types with few cones such as the rat and guinea-pig (Granit, 1947). However that may be, it is clear that although the presence of different visual mechanisms

¹ For the pupillomotor Purkinje phenomenon see further—Engelking, 1919-24; Nakayama, 1921-22; Rutgers, 1923; Laurens, 1923.

has been proved to exist which could be used for the differentiation of hues, there is no reason why the animal should not have achromatic vision. Moreover, in using electrophysiological experiments to interpret the more complex visual mechanisms such as colour vision, which presumably depends on the simultaneous recognition of unlike messages from different optic nerve fibres, conclusions cannot be based on the discharges picked up from the whole retina or optic nerve but only from the analysis of those derived from individual elements ; this was not done by the earlier workers.

(d) *Reflex responses.* Conditioned reflexes have been employed to elucidate the problem of colour vision, first by Orbeli (1909), in Pavlov's laboratory, who studied the effect of conditioned coloured stimuli on salivary secretion in dogs ; the results were inconclusive and largely negative. More conclusive evidence was obtained by Bull (1935) working on conditioned reflexes established on a basis of wave-discrimination by the blenny, *Blennius pholis*.

Other reflex responses have been utilized in the study of colour vision, such as changes in the respiration rate that occur when some fish are exposed to lights of different colours (Reeves, 1919) or changes in the reflex action of posture when the two eyes are unequally stimulated (Thibault, 1949). All such methods are of considerable corroboratory value but their results can be translated into terms of sensation only with diffidence.

(e) *The optomotor reaction* has been pressed into the service of the exploration of colour vision. Therein, it will be remembered, the animal is faced with a revolving drum with vertical stripes and if these can be differentiated, compensatory movements of the eyes occur. Schlieper (1927) reasoned that if a shade of grey were found which elicited no movements when alternated with stripes of a colour, the field must appear homogeneous and the animal must therefore be colour-blind to that colour ; from this negative response he concluded that the fishes and lizards with which he experimented only responded to differences in brightness and not in hue. Others have subsequently exploited the method, particularly Birukow (1937-50) with Amphibians, but again, the presence of a reflex response on a physical level, although suggestive, does not demonstrate the presence of colour appreciation on the physiological level.

SUBJECTIVE METHODS OF BEHAVIOURAL DISCRIMINATION are much more satisfying from the physiological point of view than objective responses since they imply the presence of the faculty to differentiate hues as sensations. Unfortunately much of the earlier work on this subject is lacking in adequate control, the principal fault being the failure to appreciate the importance of the elimination of differences in luminosity from the stimulus or, alternatively, the widespread tacit suggestion that the appreciation of luminosity (or of hue) of an animal can be legitimately equated to human sensations or to standards based on equality of energy. The assumption that the appreciation of light or colour by any species of animal resembles that of any other species, including man, rests on insecure evidence.

The simplest experimental technique is that of *colour-preference*—the simple observation of whether the animal prefers to go towards one colour before another. This crude method was first employed by Graber (1884-85) who found that certain teleostean fishes preferentially swam to a light rather than darkness, and to red rather than green rather than blue—the "step-wise phenomenon."

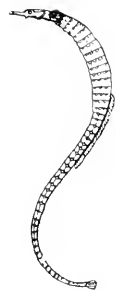
Such a technique is, of course, full of pit-falls and would lead to the conclusion, for example, that the bull recognizes and dislikes red—which has been proved untrue. In more recent years it has been superseded by the *training techniques*. The first to apply these was Zolotnitzky (1901) who fed fishes on red larvæ and then, when they had been trained to respond to this stimulus, offered them pieces of wool of different colours; they continued to choose the red, the presumption being that they appreciated it as such. Subsequently more adequately controlled techniques have been employed involving the use of T- or Y-maze experiments such as we have already described¹; their value and their limitations should again be stressed.

The COLOUR VISION OF CYCLOSTOMES is entirely unexplored.

THE COLOUR VISION OF FISHES

The colour vision of Fishes has received much attention, but none has been given to types other than Teleosteans. It is unlikely that the Selachians have colour vision with their pure-rod retinae,² but as Walls (1942) suggested, it is conceivable that among the Holosteans, *Amia*, with its duplex retina, may have been the first vertebrate type to develop colour vision. However that may be, no fish has been proved not to have colour vision, and those Teleosteans which have been investigated certainly exhibit this faculty in a considerable degree of development.

We have already noted that Graber (1884–85) first showed that the teleostean fish with which he experimented (both fresh-water, *Barbatula* and *Alburnus*, and marine, *Spinachia* and *Syngnathus*) showed a preference for certain colours, swimming towards red in preference to green and green in preference to blue, while Zolotnitzky (1901) confirmed that fish could be trained to come to red. The possibility of establishing a similar association of red with food despite variations in brightness was established by Washburn and Bentley (1906) in the dace, *Semotilus*, while Reighard (1908) found that the snapper, *Lutianus*, despite confusional variations in brightness, avoided red and preferred the shorter waves of the spectrum. This suggestion that fish were able to discriminate hues excited a considerable amount of research and not a little controversy.³ On the one hand, v. Hess (1909–22), applying the same methods of colour preference and the observation of the degree of pupillary contraction to different spectral bands, found the greatest response to the green region of the spectrum while red light elicited a poor or negative reaction; since this was typical for scotopic vision or total colour-blindness in man, he argued that fish were colour-blind, an argument fortified by his contention that, if sufficiently intense illuminations were used, an equal



Syngnathus

¹ p. 569.

² Except *Myliobatis* and *Mustelus*.

³ For summary, see Warner, 1931.

response was given to red and blue alike. This reasoning, as we have already seen, is quite invalid. On the other hand, Bauer (1909-11), working with several species (*Charax*, *Box*, *Atherina*, *Mugil*, etc.), found evidence of hue-discrimination; light-adapted fish were found to avoid red, dark-adapted specimens to prefer it, a suggestion of the presence of a Purkinje phenomenon. Shortly thereafter von Frisch (1912-25) initiated a long series of experiments based both on the dermal responses to coloured backgrounds and on training.

With a view to interpreting the significance of dermal changes to conform with the background, which are mediated through the eyes,¹ von Frisch (1912) used a species of minnow, *Phoxinus*, which changes colour *rapidly* in response to the brightness of the background and turns yellow *slowly* on a yellow-red background. He was able to match the luminosity of grey backgrounds with yellow so that the rapid change was abolished but still found that after an interval the fish turned yellow on a yellow background but never on that of a matched grey or other colour. He therefore concluded that there was a response to colour different from the response to luminosity. Further work on other species of this fish was in some cases inconclusive (Freytag, 1914), in other cases corroboratory (Haempel and Kolmer, 1914; Reeves, 1919; Schnurmann, 1920). Using the teleostean *Crenilabrus*, which reacts to red, yellow, green and blue backgrounds, v. Frisch (1912) again found that its pigment cells reacted to hue rather than brightness, a conclusion substantiated by the observations of Sumner (1911) and Mast (1916) on the teleostean flat-fishes which change their pattern of colour rapidly and dramatically to suit the changing environment while swimming over a coloured sea-bottom.²

*Phoxinus*

Final corroboration of this general conclusion has been obtained by the study of more objective responses. Reeves (1919), for example, experimenting on fish (the mud-fish, *Umbra*, and the shiner, *Notropis*), found that the respiration rate increased considerably when the illumination was increased but was more than doubled when white light was changed to red even although its intensity was simultaneously diminished—strong presumptive evidence that red was appreciated differently from white. Bull (1935), employing electric shocks to establish conditioned reflexes on the basis of hue-discrimination in the blenny, *Blennius pholis*, came to the same conclusion; while Thibault (1949), basing his observations on the fact that light exerts a tonic influence initiating a change in posture when the two eyes are unequally stimulated, brought forward striking evidence that the peripheral mechanism in the retina of the carp, *Cyprinus*, contained receptors which were individually sensitive to red, green and blue-violet.

*Blennius*¹ p. 82.² p. 92.

von Frisch (1912-25) also conducted an elaborate series of training experiments on *Phoxinus* presenting food in grey and coloured tubes or in association with grey or coloured papers. He found that his fish readily learned always to seek the colour to which they had been trained in preference to any shade of grey, even if the food were omitted so that gustatory or olfactory clues were eliminated; red and yellow tended to be confused, but blue and green were not, either between themselves or with red and yellow. This work seemed to refute the conclusions of von Hess (1909-22) based, as we have seen, on more doubtful evidence, and was corroborated on several species of Teleosts by Goldsmith (1914), White (later Hineline) (1919-27), Reeves (1919) and Hurst (1953) and on *Phoxinus* by Burkamp (1923), Schiemenz (1924), Wolff (1925), Kühn (1925) and Hamburger (1926). It has been shown that once a food-relationship had been adequately established with a particular colour, this colour is regularly sought by the fish even when the factor of luminosity has been experimentally eliminated, while Miss Reeves's experiments with a hue-discrimination box with adequate controls can only be interpreted on the thesis that the two species which she employed¹ appreciate hues as such. They can be trained to go for food to a particular colour even when its position and intensity are varied at random, and are not confused by any other colour in any degree of brightness.

This mass of experimental material suggests that the retina of teleostean fishes contains a mechanism adequate to subserve colour vision and the further conclusion would seem inescapable that these fishes are possessed of a colour sense; they appear to be able to appreciate qualitative differences between the wave-bands appreciated by us as red, yellow, green, blue, violet and the near ultra-violet (up to 365 m μ and perhaps shorter, Merker, 1934-39). From the fact that the most ready confusion exists between red and violet, it would appear that their sensations may form a closed colour-circle. The fact that they react to the human complementary mixtures of yellow and blue, red and blue-green, orange and blue-violet, and so on, as to white light suggests that their colour-system is closely akin to our own (Hamburger, 1926, in *Phoxinus*, Beniuc, 1933, in the Siamese fighting fish, *Betta splendens*).



Betta

Beniuc's technique was ingenious. He trained the fighting fish to respond positively to a grey disc and negatively to a slowly revolving disc of two complementary colours in sectors yielding grey to the human eye in rapid rotation; when the speed of revolution produced 130 sector impressions per sec. the fish responded positively as if to grey. At 90 impressions per sec. the fish reacted negatively as to separate impressions—their fusion-frequency is therefore much higher than that of man.

¹ The dace, *Semotilus*, and the sun-fish, *Lepomis*; verified by Hurst (1953) on the latter.

Although it may be thus concluded that colour vision is a definite acquisition of teleostean fishes, it is more difficult to say how far it determines their conduct in comparison with other visual sensations. The work which we have quoted, particularly that of Reeves (1919), would indicate that brightness has a greater attraction than colour, while that of Horio (1938), a Japanese investigator who combined training to different colours with different forms (triangles, discs, etc.), suggests that colour is a more clamant stimulus than form. It would seem, therefore, that as a determinant of behaviour, the colour sense takes a place intermediate between the light and the form senses.

That it does influence conduct is obvious from certain observations. Two of these may be noted. We shall see that to the male stickleback, *Gasterosteus*, the sight of red, the colour of the belly of its rival, serves as a release of the fighting response no matter what the object with which the red is associated.¹ Young jewel-fish (*Hemichromis bimaculatus*) are attracted to red, the breeding colour of the adults, and Noble and Curtis (1939) found that adult females recognized their mates as individuals by the colour-pattern on the head: if the head were painted while the rest of the body retained its natural colour, no recognition was shown, but if the entire body except the head of the male were covered, recognition readily occurred.

*Gasterosteus*

THE COLOUR VISION OF AMPHIBIANS

Investigations into the colour sense of Amphibians have been largely devoted to the Anurans. There is no doubt that from the anatomical point of view a peripheral mechanism which could subserve colour vision is present in the retina of the frog. The electroretinogram of this animal shows that a Purkinje shift exists between the light-adapted and dark-adapted eye (Himstedt and Nagel, 1902; Granit *et al.*, 1937-39), but we have already seen that this does not imply the existence of a colour sense. In the functional behaviour of this animal a phototactic response can be elicited to light which varies with the wave-length: in one species, Loeb (1890) found a negative phototactic response in which red was preferred to blue: in two other species, Torelle (1903) obtained a positive response wherein blue was preferred to red. It is to be noted that Cole (1910) found that the phototaxis of *Rana clamata* varied with the temperature. These observations, however, lead to no definite conclusion. Moreover, in the hands of the early workers training experiments invariably gave inconclusive results, probably because the learning ability of the frog is practically non-existent (Yerkes, 1903; v. Hess, 1912-22); but R. G. Smith (1948) found that by intensive training a response could be elicited in the frog, *Rana*, suggesting that a discrimination might be possible between red and blue; Thomas (1953-55), on the

*Rana*

¹ p. 665.

*Bufo**Triturus* (female)

other hand, obtained entirely negative results in training experiments involving coloured and grey papers with the toad, *Bufo*.

Subjective training experiments being thus inconclusive, we are left with evidence based on objective reflex responses. In this field the work of Birukow (1937-50) who exploited the optomotor reaction, is outstanding. Using this method he found that young tadpoles had a maximum sensitivity in the yellow region of the spectrum at all levels of illumination, while the adult frog, *Rana*, showed a Purkinje shift with a maximum sensitivity in the yellow in light-adaptation and in the green in dark-adaptation; he also found that a specific colour reaction could be obtained in this animal to red and blue, in the fire-bellied toad, *Bombina*, to yellow in addition, in the tree-frog, *Hyla arborea*, only to blue, while the toads, *Bufo* and *Alytes obstetricans*, showed no evidence of the possession of colour vision. Similarly, six species of Urodeles (*Salamandra* and *Triturus*) exhibited evidence of a differential response. Histological examination of all these Amphibians showed a duplex rod-and-cone retina. From his experiments Birukow concluded that in all cases the peripheral mechanism for colour vision was equally present and that the lack in those species which appeared to be colour-blind was in the central mechanism. When colour-deficiency occurred it would seem that yellow and yellow-green were the first colours to be missing, leaving a neutral region in the centre of the spectrum, then red and blue-green, and finally blue. Whether these reactions are associated with sensations is another question, and in the meantime it would be wise to conclude that, although the required mechanism may be present, there is little evidence that sensations of colour enter prominently into the behaviour of Amphibians.

THE COLOUR VISION OF REPTILES

Our knowledge of the colour vision of Reptiles is meagre, partly because of the paucity of research done on the question and partly because of the difficulty of using such animals as subjects in behavioural experiments. The colour appreciation of *Sphenodon* has been unexplored; among the Crocodilians it would seem from the evidence of pupillary contraction that a Purkinje shift occurs between a maximum sensitivity of 544 $m\mu$ in light-adaptation to 514 $m\mu$ in dark-adaptation (Laurens, 1923); while some snakes appear to be amenable to colour training experiments (Kahmann, 1931; Grodzinska, 1948, on the grass-snake, *Tropidonotus*). Sufficient work, however, has not been done with these reptiles to allow us to draw any pragmatic conclusions.

Some training experiments have yielded positive results with Chelonians and Lacertilians. v. Hess (1913) found that turtles showed spontaneous colour-preferences, while Wojtusiak (1933), Quaranta

(1949) and Quaranta and Evans (1949) have shown that tortoises (*Clemmys*, *Testudo*) can with perseverance be made responsive to training techniques and therein show discrimination between blue, green and orange ; as in fishes, red is apparently readily confused with violet. So far as lizards are concerned, Schlieper's (1927) experiments with *Lacerta vivipara* using the optomotor reaction gave negative results ; a positive response was elicited only by differences in brightness. Musloff (1955) had a similar experience with *Anguis* and the nocturnal gecko, *Hemidactylus*. Wagner (1932), on the other hand, in training experiments using coloured papers associated as positive stimuli with food or as negative stimuli with salt (which the lizard violently dislikes), obtained evidence that colours were differentiated from white or greys and that separate appreciation could be made of red, yellow, green and blue ; this finding was corroborated in *Anolis* for red, yellow-green and green but not for yellow and blue by Musloff (1955) using the optomotor reaction as a criterion. It would appear, therefore, that those Reptiles that have been investigated show the potentiality of colour vision and that some lizards can base their behaviour upon it.

*Testudo**Anguis**Hemidactylus*

THE COLOUR VISION OF BIRDS

That Birds possess a highly developed colour sense has always been accepted partly because the bright colours of their plumage obviously adopted as an attraction in mating would otherwise be biologically inexplicable.¹ and partly because of the proven ability of some of them to pick out preferentially coloured flowers and fruit for feeding. Recent experimental work has demonstrated beyond question that this is indeed the case.

The first scientific investigations were objective in nature. The electroretinogram was utilized by Piper (1905) who showed that in diurnal types such as the hen the maximal response occurred to wavelengths of 600 m μ . in nocturnal types such as the owl, to 535 m μ ; he concluded that neither type itself showed an individual Purkinje shift but that this phenomenon could be demonstrated between the two types. Shortly thereafter Abelsdorff (1907) and subsequently Laurens (1923) and Erhard (1924) made a similar study on the differential contraction of the pupil when the eye was illuminated by various spectral bands and it was shown that a Purkinje phenomenon could be elicited in a diurnal bird (the pigeon) provided an unusually long time (45 mins.) was allowed for dark-adaptation to develop. From an analysis of their data these authors concluded that the mechanism necessary for hue-discrimination existed and in general resembled that found in man, but the illegitimacy of these conclusions we have already stressed.

¹ p. 104.

The somewhat surprising suggestion was, however, put forward by Vanderplank (1934) that the pupil of the tawny owl, *Strix*, contracted to long infra-red rays (900 m μ) far beyond the limits of human visibility, the idea being that this bird "saw" its prey in the dark by means of the latter's body-heat. This, however, has been refuted by Hecht and Pirenne (1940) in another species of owl, *Asio*, while Matthews and Matthews (1939) showed that the ocular media of *Strix* absorbed completely all the infra-red radiation in this spectral area. It may therefore be accepted that the objective evidence indicates that the photochemical system of the eyes of Birds is similar to that of man.



Sparrow

Behavioural experiments have borne out the same conclusion in a very definite way although they have been somewhat handicapped by the essential stupidity of birds. That colour vision does influence their behaviour was shown by the early experiments of Lloyd Morgan (1896) with chickens, Porter (1904-6) with the sparrow and Rouse (1906) with the pigeon; these birds all show a preference for certain colours and can be trained by food-association to pick them out. The most elaborate investigations, however, were undertaken by Carl von Hess (1912) who experimented both with diurnal (chickens, pigeons) and nocturnal birds (owls). He found that chickens, for example, picked up grains of rice illuminated on a white ground by spectral lights from the red end of the spectrum to the green but refused those illuminated with blue light; he therefore concluded that this bird had colour vision but that the spectrum was much shortened at the short-waved end and that the fowl was blue-blind. It is interesting in this connection that in contrast to the yellow, blue or white flowers preferentially pollinated by bees,¹ the usual bird-pollinated flowers are red (Werth, 1915; Pickens, 1930; Porsch, 1931). This suggestion of blue-blindness, although supported by Henning (1920), has not stood the test of time, for it has been subsequently shown that the hen and many other species can see blue and violet, but that training is necessary if the bird is not to reject a food coloured quite unlike anything in nature; there is, however, a certain degree of blue-violet-weakness, probably because of the absorption of short-waved light by the retinal oil-droplets (Watson, 1915; Lashley, 1916; Hahn, 1916; Honigmann, 1921; Blässer, 1926; Bailey and Riley, 1931; Hamilton and Coleman, 1933; Plath, 1935; and others). It would seem clear that the limits of spectral visibility and the discrimination of hues resemble those of man; that the colour-vision system might possibly be interpreted on a trichromatic basis²; that a relatively small number of hues are distinguishable (20 by the pigeon in contrast with 160 by man, Hamilton and Coleman, 1933); while by training birds to peck

¹ p. 587.

² It is always to be remembered that by *trichromatic vision* is meant the ability to match all colours with a mixture of three, and only three, primary colours. This must involve colour-mixing experiments and without these it is illegitimate to draw any conclusions as to the number of mechanisms involved.

from coloured pieces of paper on large grey backgrounds, Révész (1921) showed that the phenomenon of simultaneous contrast could be elicited as in man. It would seem, indeed, that while the behaviour of Birds is largely determined by vision, they rely more upon the discrimination of hue than of luminosity, and respond more consistently to clues involving colour than those depending on form (Jones, 1954).

The appreciation of "warning colours" displayed by insects illustrates the biological value of colour vision to the bird in its feeding habits. In experiments with the swallow, *Hirundo*, Swynnerton described vividly how one bird would watch another intently, observing its reaction to a new test-insect of a particular colour as if with the intention of profiting thereby by avoiding the unpleasant experience of eating a distasteful species. In the same way birds such as the domestic hen can be trained to tasks involving the discrimination of colour as well as of size and form, both singly and in combination (see Altevogt, 1951; Thorpe, 1956).



Swallow

The colour vision of Birds must be considerably modified by the presence of COLOURED OIL-DROPLETS, a circumstance which must also apply to other species similarly equipped.¹ Initially, owing to the inferior quality of the earlier lenses in the microscopes employed in histological work, droplets of a much larger range of spectral hues—green, blue and violet—were described in the retina of birds, and Krause (1863) put forward the theory that this coloured mosaic represented a peripheral mechanism whereby colour vision could be determined in the avian eye by the absorption of all wave-lengths except one by a particular droplet so that different cones were stimulated only by a single narrow spectral band of light. This theory held the field for many years. Convincing arguments, however, can be advanced against it for oil-droplets are by no means necessary for colour vision: fishes (and man) have colour vision and no coloured droplets; lizards have a colour-system of considerable complexity and only yellow droplets; the fovea of birds with its excellent appreciation of colour has yellow droplets only; and in the periphery of the avian retina the colours of the droplets bear no relation to the spectral range of the bird. It is much more likely, as Walls and Judd (1933) suggested, that these droplets, whatever their colour, act as filters with the triple function of increasing contrast, reducing glare and lessening chromatic aberration—that they are, in fact, an aid to visual acuity.

The yellow droplet at the avian fovea, cutting off the spectrum at 515–520 mμ like a yellow-tinted spectacle, allows the transmission of many hues but

¹ It may be useful to summarize the occurrence of oil-droplets in the visual elements of Vertebrates at this point. They are found in the rods of *Lepidosiren*; in the cones of Chondrosteans, the coelacanth and *Protopterus* (all colourless), diurnal Anurans (yellow), lizards (yellow; some nocturnal types colourless or none), Chelonians (orange, yellow, red), *Sphenodon* (colourless or pale yellow), Birds (red, orange, yellow, occasionally green or colourless), the platypus (colourless), and Marsupials (except some Didelphyidae) (colourless).

eliminates most of the violet and some of the blue, thus diminishing glare and at the same time considerably reducing chromatic aberration, a phenomenon for which these wave-lengths are partly responsible. This colour of droplet is thus found preferentially in the central and ventral parts of the retina where it must increase acuity and enhance contrast by eliminating the preponderating and dazzling blue light of the sky. The reduced sensitivity to blue light of the chicken and other species remarked upon above is thus explained, as well (perhaps) as the tendency of such birds as pollinate flowers (humming-birds, honey-birds) to choose preferentially red blooms. The red droplets, cutting off the spectrum at 580–590 $m\mu$, will be particularly valuable in damping down the excessive long-waved light at sunrise or sunset (hence their large numbers in early-rising song birds in which they comprise 20% of the total); they will have a similar effect on the light of long wave-lengths reflected from the water (hence their presence in quantity in turtles or the kingfisher); they will be of less value in other optical conditions (hence their paucity—3 to 5%—in late-rising crepuscular types such as swifts or swallows); while their preferential occurrence in the dorsal part of the retina will give maximal contrasts to objects seen against a green background. The orange droplets will provide a transition between the two.

It would seem, therefore, that the oil-droplets have no part in the mechanism of colour vision, but at the same time they must influence the appearance of coloured objects so that the bird's appreciation of them ought to be quite different from ours. To birds that possess them, central vision probably resembles vision through yellow spectacles, while elsewhere in the retina with the constant sudden movements of the head, each object is scanned and analysed now through one filter, now through another, the kaleidoscopic changes allowing an unusually high discrimination of tone and necessarily increasing contrast and therefore the visibility of details.¹ Looking through this polychromatic mosaic, a bird should be able to distinguish objects invisible to us: thus Judd found that a bird could readily pick up crickets mixed deliberately with dry leaves although he could not differentiate between them, while Rabaud (1920) noted that sparrows saw at once and ate green phasmids, which as far as he was concerned mimicked perfectly the leaves on which they rested.

THE COLOUR VISION OF MAMMALS

As we would expect from the rarity of strongly diurnal Mammals, the possession of colour vision by the members of this class is apparently rare. The more primitive and nocturnal types are colour-blind; some of the arhythmic types may possess some degree of hue-discrimination but this faculty plays a small part in their behaviour, being completely subservient to sensations of luminosity; only the higher Primates have a colour sense sufficiently developed to influence their activities to an extent that can be experimentally elicited with certainty.

Of the colour vision of MONOTREMES we know nothing; among MARSUPIALS, Sälzle (1936) reported negative results with the opossum,

¹ See further p. 662.

Didelphys. Among INSECTIVORES, only the hedgehog, *Erinaceus*, has been examined ; in experiments wherein brightness-differences were inadequately controlled, Herter and Sgonina (1933-34) suggested that this animal could see yellow as distinct from grey, but on the evidence this conclusion seems unjustified.

Among the RODENTS a considerable number of species has received experimental attention. The *rat*, with its nocturnal habits, its practical absence of cones and complete absence of a Purkinje phenomenon as measured pupilloscopically or electroretinographically, would not be expected to possess a colour sense. Training experiments with spectral lights (Watson and Watson, 1913) or coloured papers (Munn, 1932 ; Coleman and Hamilton, 1933 ; Muenzinger and Reynolds, 1936) have verified this expectation. The work of Walton (1933), Walton and Bornemeier (1938) and Caïn and Extremet (1954), however, suggested the opposite conclusion—that this animal could make choices on the basis of hue-discrimination particularly between red and green ; but this view is unique. Similarly negative results were obtained by training experiments in domestic *mice* (Yerkes, 1907 ; Trincker and Brendt, 1957) but again, one investigator, Hopkins (1927), claimed that 1 mouse in 7 could distinguish red from white. Wild mice were investigated by Sälzle (1936) ; one variety, the European field-mouse, *Apodemus*, showed no evidence of colour vision, but the red-backed vole, *Clethrionomys*, could, in his view, discriminate between red and green, although not between green, yellow and blue. In the reports of these experiments, however, the control of the intensity of stimulation is vague. A similar criticism applies to the study of the *guinea-pig* by Sgonina (1936) who assumed that this animal had the same appreciation of brightness as he himself ; but in well-controlled experiments using the optomotor reaction, Trincker and Berndt (1957) obtained different responses with red, yellow, green and blue. Completely negative results were obtained in the *rabbit* by Washburn and Abbot (1912) and in the *porcupine* by Sackett (1913). The evidence therefore points to the conclusion that these rod-rich nocturnal rodents, all of which show a low sensitivity to red light, have achromatic vision.

It would be expected that the highly diurnal *squirrel* with its cone-rich retina would be in a different case. Here the evidence is confusing. In experiments in which brightness was considered analogous to its appreciation by the human experimenter, Colvin and Burford (1909) and Sälzle (1936) concluded that the European tree-squirrel, *Sciurus vulgaris*, could discriminate hues ; but in more adequately controlled work Locher (1933) found that one squirrel out of three could with great difficulty be trained to differentiate yellow and light green ; all other colours were equated with different shades of grey. Meyer-Oehme (1956), on the other hand, claimed that squirrels



Hedgehog



Porcupine

could be trained in behavioural experiments to distinguish red, yellow, green and blue papers from one another and from grey of equal brightness. With the European ground-squirrel (souslik, *Citellus citellus*), Kolosváry (1934) concluded that a colour-preference existed for blue. None of these experiments is fully convincing, but it seems that a weak capacity for colour vision may exist in some species of squirrel, while in many individuals it is wholly absent; even if it is occasionally present, it seems unlikely that it can determine behaviour.

Among the CARNIVORES, the earlier workers gave most attention to the *dog*. The variable results initially obtained are vitiated by absence of the adequate control of intensity (Lubbock, 1888; Gates, 1895; Himstedt and Nagel, 1902; Nicolai, 1907; Orbeli, 1909; Colvin and Burford, 1909; Kalischer, 1909); while the better controlled experiments of Samoiloff and Pheophilaktova (1907) and E. M. Smith (1912) led to the conclusion that hues have little significance for this animal despite its undoubted intelligence and amenability to experimental restraints. Confusion of coloured papers with greys was practically constant although after prolonged training some animals seemed to show some recognition of green. It will be remembered that Orbeli (1909) in Pavlov's laboratory, found similarly inconclusive results on attempting to establish conditioned reflexes to colours in this animal.¹ All observers are agreed that colours have no significance whatever for the *cat*, whether attempts at training have been made by coloured papers or spectral lights (de Voss and Ganson, 1915; Gregg *et al.*, 1929; Gunter, 1952-54; Meyer *et al.*, 1954); the positive results claimed by Colvin and Burford (1909) and Kalischer (1909) can be explained by inadequate controls and the mistake of equating relative brightness to human standards. A similar criticism applies to the claim of Cole (1907) and Cole and Long (1909) that the *raccoon* has some degree of colour vision; Davis (1907) and Gregg and his co-workers (1929) obtained completely negative results with this animal, as did Müller (1930) in the marten, *Martes*, and the pole-cat, *Putorius*. It would seem, therefore, that with the problematical exception of the *dog*,² all the Carnivores so far tested have proved to be colour-blind or have indicated that colours have no significance for them. If in some dogs some discrimination of hue is possible, the faculty seems to be without importance to the animal and is entirely dominated by sensations of form and brightness.

UNGULATES which have been investigated have been found to be similar. *Cattle*—even the fighting bulls of Latin Europe and America—are completely colour-blind (Kittredge, 1923; Stratton, 1923); they

¹ p. 623.

² See, however, Schubert (1950) who, while admitting that it has not been shown experimentally that dogs have hue-discrimination analogous to man, insists that these animals are not colour-blind.

are enraged by the flutter, not the colour of the matador's cloak and equally enraged whether it be red, green, grey or white. Grzimek (1952), on the other hand, from feeding experiments wherein colours were matched with shades of grey, claimed that the *horse* possessed a considerable degree of colour vision, best for green and yellow and least for red.

PRIMATES are the only order among the Mammalia in which colour vision exists as a factor capable of determining behaviour, and within this class this applies only to the higher diurnal species. Most of the lower Primates are nocturnal, but even the diurnal lemur has been shown to be either totally colour-blind, confusing all colours with greys, or to possess a colour sense so meagre as to be valueless, comparable to that which may exist in some dogs (*Lemur mongoz*, Bierens de Haan and Frima, 1930). Among the Anthropoidea, on the other hand, colour vision begins to become evident. The primitive capuchins (*Cebus*) are of particular interest since they appear to show a dichromatic colour system corresponding to a protanopic deficiency in man with a lowered sensitivity to red (Watson, 1909; Grether, 1939). The marmosets have not been studied from this point of view; but the higher Simians all show a well-developed chromatic system, both the New World Platyrrhines and the Old World Catarrhines and Apes.¹



Lemur

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¹ The spider monkey, *Ateles*, the baboon, *Papio*, the macaque, *Nemestrinus*, the langur, *Pithecius*, the rhesus monkey, *Macaca rhesus*, the mangabey, *Cercocebus*, and the chimpanzee, *Pan* (Kimaman, 1902; Kohler, 1918; Kohts, 1918; Trendelenburg and Schmidt, 1930; Klüver, 1933; Brecher, 1936; Grether, 1939-41).

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THE PERCEPTION OF FORM

As we have already seen, the visual acuity of most Vertebrates (with marked exceptions) is low; in the activities of animal life greater reliance is generally placed on the appreciation of differences of luminosity and movement. Although on this account the eye may often be a relatively poor optical instrument in the resolution of imagery, that is not to say by any means that it is not biologically useful; to many Vertebrates living in an aquatic or nocturnal environment or close to the ground with a restricted horizon, the appreciation of luminosity and movement must be much more valuable than an ability to resolve minutiae in form, nor would an eye capable of recording elaborate patterns be of biological utility without a brain sufficiently evolved to analyse and appreciate and utilize such impressions.

Apart from the ability of the brain to analyse and appreciate

visual patterns, the acuity of vision depends on two factors—the size and optical perfection of the retinal image and the resolving power of the retina. So far as optical factors are concerned, the larger the eye, the larger and therefore the more analysable the image; the more transparent the media and the more perfect the refracting system, the higher its resolution; and if objects at different distances are to be imaged with equal clarity, an efficient accommodative mechanism is a necessity. So far as the retinal factors are concerned, the denser the mosaic of recipient elements and the lower the ratio of these to the optic nerve fibres (which usually means the greater the number of cones), the higher the resolving power of the retina. Before assessing the importance of visual acuity to the vertebrate world we shall take note of these physical factors on which its effectivity is based.

THE OPTICAL SYSTEM

THE REFRACTION OF VERTEBRATES

A considerable amount of work has been devoted to the estimation of the static refractive system in Vertebrates, the more important results of which are summarized below.

CYCLOSTOMES—The lamprey is myopic to the extent of -8 D in water, a refraction suitable for a parasitic creature.

FISHES—It is generally agreed that **SELACHIANS** are all strongly hypermetropic (in water), the refraction varying from $+8$ to $+15$ D with some astigmatism (Rochon-Duvigneaud, 1918; Verrier, 1928–35; Franz, 1931).

In **TELEOSTEANS**, however, the position is not so clear. Beer (1894) was the first to study this question intensively; by retinoscopy he found the eyes of several species to be hypermetropic but he discarded these results in favour of a theoretical analysis of the dioptric system of the eye, which led him to conclude that the teleostean eye showed a degree of myopia varying in different species from -3 D to -12 D in water (-40 to -90 D in air), a result confirmed or accepted by most subsequent writers (Franz, 1931). On the other hand, Rochon-Duvigneaud (1918) and Verrier (1928), using retinoscopy under water, reaffirmed the presence of a hypermetropia of $+8$ or $+9$ D in a number of species of pelagic fishes, and Verrier (1938), placing a screen in the coats of the eye at the posterior pole, found that a sharp image of a luminous cross could not be obtained at a distance less than 40 cm. under water; she therefore questioned the accepted view that myopia was characteristic of Teleosteans. Her results were accepted by Rochon-Duvigneaud (1943) in preference to those of Beer; but the optical problem is difficult and the position is obscure. It would seem probable that some Teleosteans are hypermetropic while some may be myopic, particularly deep-sea types wherein a myopia may be present up to -12 or -15 D. In this connection it is to be remembered that myopia would be a useful refraction for a fish, for vision under water at any considerable distance is impossible in any case.

AMPHIBIANS—Among Anurans the refraction of the frog has received most study: the animal is essentially terrestrial in its visual habits. In air, retinoscopy shows a hypermetropic error of the order of $+3$ D with $+2$ D of astigmatism

with the axis vertical. If, however, a theoretical correction is made for the difference of level between the reflecting surface of the retina and the layer of rods and cones, Hirschberg (1882) concluded that the hypermetropia became converted into a myopia of the order of -5 to -8 D; Beer (1898), on the other hand, assumed a smaller degree of myopia. Under water, of course, with the elimination of the corneal refraction, a high degree of hypermetropia results ($+16$ D, Hirschberg; $+25$ D, Beer).

The refraction of Urodeles seems to be suited to their usual environment. Among aquatic Urodeles the newt is approximately emmetropic under water and strongly myopic in air, while terrestrial salamanders tend to be approximately emmetropic in air.

REPTILES. Little is known of the refraction of Reptiles. In freshly decapitated lizards Kahmann (1932) usually found a low degree of hypermetropia, up to $+6$ D in *Lacerta agilis*. The Crocodilians are slightly hypermetropic in air ($+7$ to $+8$ D, Abelsdorff, 1898; $+1$ to $+2$ D, Rochon-Duvigneaud, 1943, in the alligator); they are therefore highly hypermetropic under water. Most turtles are emmetropic, the marine species in water, the terrestrial in air. According to Beer (1898) snakes are usually hypermetropic (up to $+9$ D).

BIRDS. The majority of Birds on which retinoscopy has been undertaken has been found to be emmetropic or slightly hypermetropic, the notable exception being the kiwi, *Apteryx*, which is myopic (Rochon-Duvigneaud, 1943); the aquatic penguins are also myopic in air.

MAMMALS. In the overwhelming majority of Mammals in the wild state the refraction is slightly hypermetropic (under 1 D); a hypermetropia of greater degree ($+2$ to $+5$ D) is found in some Marsupials, Edentates and Rodents in natural surroundings, while in the many small Mammals equipped with small eyes containing a relatively large lens closely approximating the retina, the hypermetropia may increase up to $+7$ or $+10$ D. Most of such Mammals (as the mouse) are nocturnal in type and obviously depend visually on the appreciation of differences in luminosity and movement rather than on the very imperfect pattern-vision of which their eyes are capable. The similarly-sized squirrel, on the other hand, which is highly visual in its habits, is practically emmetropic in natural surroundings. The unique eyes of the bats (Chiroptera) are likewise strongly hypermetropic ($+15$ D, Rochon-Duvigneaud, 1943). Myopia in wild and natural conditions is rare and sporadic, being confined essentially to some Primates (mandrills and baboons) and amphibious types—Sirenians (the dugong is -5 D in air but strongly hypermetropic in water) and Pinnipedes (seals, sea-lions). Thus the seal may have -4 D of myopia combined with -9 D of astigmatism with the axis vertical (Johnson, 1901). According to Matthiessen (1886-93) the whale, the eyes of which are fully adapted for aquatic vision, is slightly hypermetropic in water; in air, of course, it is highly myopic while the asymmetry of the corneal curvature (neutralized under water) results in a considerable degree of astigmatism (4 to 4.5 D). Ungulates are generally emmetropic but tend to have some horizontal astigmatism, perhaps an adaptation to extend the horizontal visual field. Thus most horses are emmetropic with small variations towards hypermetropia, myopia or astigmatism (Rochon-Duvigneaud, 1943). Similarly dogs and cats have a smaller range of refraction than man; the majority are emmetropic or nearly so and a high refractive error is a rarity (above $+2$ D), although errors of the order of 4 D are found more commonly in myopia than hypermetropia. Among domestic animals, however, the refractive error tends to vary considerably in all directions of error; thus many animals kept in hutches such as rabbits, guinea-pigs and so on, often develop a high degree of myopia.

ACCOMMODATION IN VERTEBRATES

While an emmetropic static refraction is necessary for the attainment of a high degree of visual acuity, the capacity to adjust the optical system for near or distant vision is almost equally important, particularly in such activities as the capture of prey. In an amphibious life if any adjustment to the two environments is attempted the importance of accommodation is still greater owing to the difference in refractivity between water and air; in an active arboreal life a rapid and effective adjustment becomes vital for safety; while the need for close examination of objects manipulated by the hands becomes of crucial importance in the activities of the higher Primates and man.

Few vertebrate species are entirely without accommodation, and to these vision is invariably of little biological importance. Such a mechanism is lacking in the extant representatives of the primitive groups of Fishes—Chondrosteans, Dipnoans¹ and the coelacanth; the function of the campanular muscle of Holosteans has not been explored. Among Amphibians and Sauropsidans an accommodative mechanism is present except perhaps in *Sphenodon*. Owing to their nocturnal habits, accommodation is lacking or exceedingly feeble in primitive Mammals. It is absent in Monotremes, and although a ciliary muscle is present in Marsupials, no accommodation has been demonstrated in any species of this group. In the lower Placentals accommodative activity is similarly lacking for the ciliary muscle is vestigial if, indeed, it is present (except in squirrels); even Ungulates such as the horse, sheep and pig have no demonstrable dynamic accommodation, and apart from the feeble accommodation of squirrels and Carnivores, an effective range is found among Mammals only in the otter and in the Primates, particularly in man.

Within the vertebrate phylum accommodation is achieved by a great variety of devices; it would appear as if at one time or another in the various species every conceivable means of adjusting the dioptric system of the eye to various distances had been attempted. These varying expedients may be classified into two types—static devices whereby optical elasticity is achieved by structural peculiarities; and dynamic devices depending upon an active alteration in the dioptric system brought about by muscular activity.

Static Devices

In the first place, it is to be remembered that a *small eye* to a large extent obviates the need for an active accommodative mechanism. A small lens with a short focal length has a greater depth of focus than

¹ The eye of *Neoceratodus* is unexplored from this point of view.

a large lens, while in the retina of such an eye the visual elements are relatively large so that the image still falls on the rods and cones even although it suffers a considerable (relative) excursion. It is probable, indeed, that small eyes (as are typical of the more primitive Placentals which are without accommodative adjustment) have a range of vision as great as the large eyes of most of the more highly developed Carnivores.

In many cases, however, specific expedients are found which provide a varying degree of accommodative elasticity, some of them probably incidental, others obviously adapted for the purpose. These may concern the optical system of the eye or the retina. Among these the more important are :

(a) A *stenopaïc pupil* is primarily a protective adaptation against excessive light, but at the same time it converts the optical system of the eye into that of a pin-hole camera in which accommodative adjustment is unnecessary—a simple expedient which, however, suffers from the disadvantage that the available light reaching the retina is cut down in proportion as the diminution of the aperture becomes effective. For purely mechanical reasons such a stenopaïc aperture is more readily and therefore more frequently attained by the development of a slit-pupil than a small circular pupil which requires a difficult muscular effort.¹ Since it abolishes the necessity for accommodation this method is most dramatically employed as a means of overcoming the enormous accommodative adjustment required to bridge the refractive difference between aquatic and aerial vision, as in seals or sea-snakes.²

(b) A *duplicated optical system* may be employed, a device adopted by various amphibious Vertebrates to overcome the large step between aerial and aquatic vision. This is attained by an optical asymmetry of the lens which is pyriform in shape so that it is emmetropic in one axis and hypermetropic in the other. Among Fishes the use of the appropriate system is ensured in *Anableps* by the presence of two pupils.³ It will be remembered that this fish swims in such a way that the water-line cuts the middle of the cornea ; the upper pupil, subserving aerial vision, admits a pencil of light along the shorter axis of the lens to focus on the lower part of the retina, the lower pupil which is submerged is optically associated with the long axis of the lens and the upper part of the retina (Fig. 766). A somewhat analogous arrangement is seen in the kingfisher. *Alcedo*, which is provided with two foveæ, a central for use in aerial vision, and a second situated in the far temporal periphery somewhat evaginated in an out-pocket of the sclera. The lens is egg-shaped with its narrow end pointing to

¹ p. 612.

² p. 649.

³ Compare the dorsal and ventral compound eyes of the whirligig beetle, p. 244.

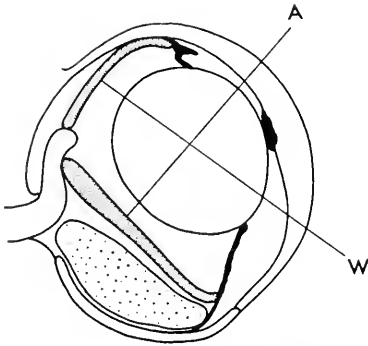


FIG. 766.—The eye of *Anableps*.

Because of the pyriform shape of the lens the upper pupil and lower retina are positioned for aerial vision (A), the lower pupil and upper retina for aquatic vision (W) (c.f., Fig. 385).

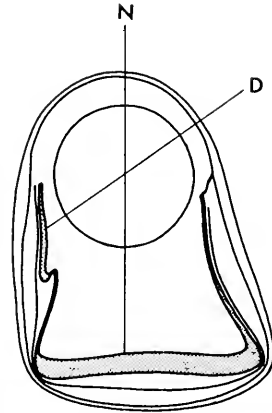
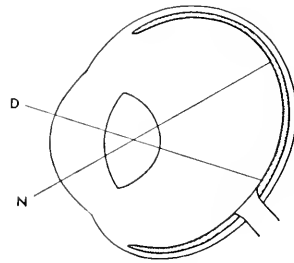
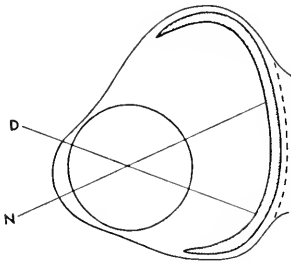


FIG. 767.—The tubular eye of a deep-sea fish.

The main retina is used for near vision with a myopic optical system (N); the accessory retina for distance vision with a hypermetropic optical system (D).



FIGS. 768 AND 769.—The ramp-retina.

FIG. 768.—The eye of the ray.

FIG. 769.—The eye of the horse.

In each case distance vision is subserved by rays striking the lower (hypermetropic) part of the retina (D); near vision is subserved by rays striking the upper (myopic) part of the retina (N).

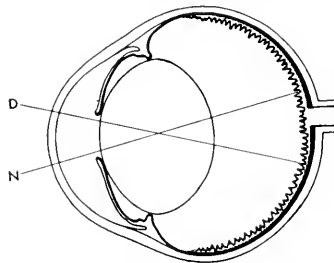


FIG. 770.—The eye of the fruit bat.

Distance vision is subserved by retinal elements at the top of a papilla (D); vision by elements in the trough between two papillae (N) (c.f., Fig. 581).

the temporal fovea and its long axis running parallel to the palpebral fissure so that the refraction through this axis is extremely myopic ; this system is brought into play for aquatic vision when the bird dives under water for its prey (Kolmer, 1924).¹

(c) *An extraneous alteration of the optical system by the interposition of the nictitating membrane.* This is a curious and unique mechanism seen in diving ducks, loons and auks whereby the third eyelid is brought over the cornea when the bird is immersed ; the nictitating membrane has a transparent window with a high refractivity, so that when it is interposed in the visual axis the already powerful intra-ocular accommodative mechanism is augmented.

(d) *A duplicated retina* is a rare accommodative expedient seen in the tubular eyes of some deep-sea fishes in which the relatively enormous size of the spherical lens precludes any effective accommodative adjustment² : the principal retina in the axial position is myopic compared with the accessory retina situated close to the side of the lens (Fig. 767). In addition to this static mechanism we shall see presently that there is a supplementary dynamic component mediated by a muscle of accommodation.³

(e) *A sloping ramp-retina* is a somewhat similar device whereby the axial length of the globe changes continuously in the vertical direction, being progressively further away from the lens in its superior segment. Such a configuration is seen in some Selachians (*Raja*) (Fig. 768) and particularly in Ungulates (Franz, 1934). In the horse, for example, which has no dynamic accommodation, the axial retina which is used for forward regard is emmetropic while the upper portion of the retina, used for the near vision required in grazing, is myopic (Fig. 769). A somewhat similar arrangement is seen in the ocelli of some Invertebrates.⁴

(f) *The corrugated retina* of the larger bats (Megachiroptera)⁵ results in a considerable variation in the distance of the receptor elements from the optical centre depending on whether they are situated on the crests or the sides of a choroidal papilla or in the valleys between them ; from the optical point of view this must ensure that the images of objects situated at varying distances will be focused on some visual cells (Fig. 770).

(g) *An unusual length of the receptor elements* of the retina will have the same optical effect for the image, while yet remaining within the receptor layer, will be able to traverse a considerable axial distance corresponding to a relatively great movement of an object in space. An extreme length of the visual elements, as is seen in many deep-sea Teleosts or in nocturnal geckos (Fig. 433), is doubtless primarily an

¹ p. 655.

⁴ Fig. 106.

² p. 323.

⁵ p. 459.

³ p. 646.

adaptation to increase sensitivity to light¹; but some accommodative elasticity is thereby also rendered possible.

Dynamic Devices

Dynamic accommodation involves one of two expedients—a movement of the lens as a whole or its deformation; both are brought about by muscular activity and in every case the essential muscles involved are under the control of the oculomotor nerve. In the first case the lens may either be pushed or pulled backwards or forwards; in the second it can be deformed by direct pressure or in an indirect way through varying the tautness of an elastic capsule.

An accommodative function has been ascribed to two other devices on more questionable grounds. It has been claimed that the columns of connective and muscle tissue traversing the thickness of the choroid of Birds may pull the retina backwards.² Such an axial movement of the retina as an aid to accommodation is, however, by no means established. A still more questionable hypothesis is that the pecten of Birds serves as an adjuvant to accommodation.³

(a) *A movement of the lens as a whole.* This mechanism is characteristic of the more primitive Vertebrates. The firm spherical lens of high refractive index necessary for optical purposes in an aquatic environment is obviously not easily susceptible to deformation; this mechanism is therefore seen in Cyclostomes and Fishes and has been retained by Amphibians; it also occurs in snakes, the eyes of which, as we have remarked,⁴ are essentially primitive in most of their characteristics. It is to be noted, however, that in the last an entirely

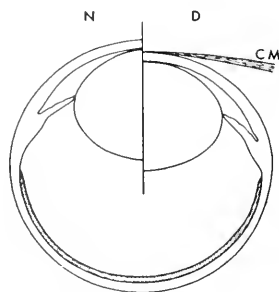


FIG. 77L.—ACCOMMODATION IN CYCLOSTOMES.

N, the eye adjusted for near vision; D, the eye adjusted for distance vision. The corneal muscle, CM, pulls the cornea backwards which in turn pushes the lens nearer the retina.

novel and distinct technique has been evolved bearing no relation to the ichthyopsidan plan. If the lens is moved backwards the eye becomes hypermetropic and vision is adjusted for distant objects (negative accommodation); this is characteristic of Cyclostomes and Teleosteans. If the lens is moved forwards the eye is rendered myopic and accommodation is attained for near vision; this is seen in Selachians and Amphibians; the same direction of movement is also seen in snakes.

(i) *A backward movement of the lens induced by corneal pressure.* This mechanism is seen only in the most primitive of Vertebrates—the CYCLOSTOMES; to these it is unique and an intra-ocular accommodative

¹ pp. 305, 364.

³ p. 416.

² p. 404.

⁴ p. 383.

mechanism is lacking (Fig. 771). In the lamprey the cornealis muscle¹ which lies outside the orbit and is inserted into the dermal part of the cornea, draws the cornea taut as it contracts, flattens it and thus presses the lens, which lies in contact with this tissue, backwards to approach the retina. It may be that a contraction of the extra-ocular muscles

FIGS. 772 TO 776.—ACCOMMODATION IN TELEOSTS.

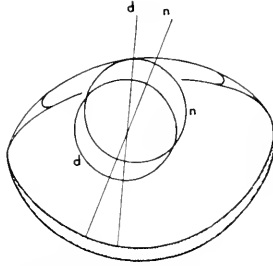


FIG. 772.—A change in position of the lens : in relaxation for near, *n*, and in accommodation for distance vision, *d*.

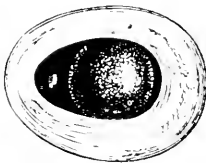


FIG. 773.

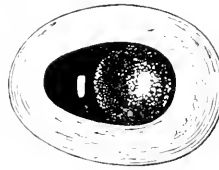


FIG. 774.

FIGS. 773 AND 774.—The left eye of the sea-bass, *Serranus cabrilla* (after Beer).

Showing the aphakic area in the pupil in which can be seen the inverted retinal image of a gas flame situated in the temporal part of the eye. Fig. 773, at rest ; Fig. 774, in active accommodation.



FIG. 775.



FIG. 776.

FIGS. 775 AND 776.—The left eye of the blenny, *Blennius sanguinolentis* (after Beer).

Fig. 775, at rest ; Fig. 776, in active accommodation (seen from above the fish).

which jacket the globe has the opposite effect of elongating it to aid the relaxation of accommodation : but this is conjectural. The spherical lens, wedged between the cornea in front, the relatively solid vitreous behind and the immobile iris at the sides, has no suspensory apparatus. This mechanism of accommodation is both simple and effective,

¹ p. 271.

providing accommodation for distant objects and giving the normally myopic eye a fairly high degree of hypermetropia ; Franz (1934) claimed that the extraordinarily wide range of accommodation from + 20 to - 20 D is thus rendered available.

(ii) *A backward (and sideways) movement of the lens induced by direct muscular action* as an accommodative mechanism for distant vision is unique to TELEOSTEAN FISHES among which it is of general occurrence, although it is absent or ineffective in very small-eyed forms which have a relatively large lens. The classical view put forward by Beer (1894) and confirmed by most authors (Franz, 1905-31 ; Meader, 1936 ; Rochon-Duvigneaud, 1943) is the following (Fig. 772). As in the lamprey, the spherical lens normally approximates the cornea, suspended naso-dorsally by a zonular ligament on which it can swing pendulum-like backwards and forwards. A backward movement is brought about by the retractor lentis muscle (the campanula of Haller), a small ectodermal muscle situated naso-ventrally derived from the ectoderm at the borders of the falciform process.¹ It is to be noted that in the act of accommodation the lens moves as much temporally (towards the tail) as backward into the eye, if not more so, thus moving the image sideways across the retina ; by this movement the image will leave the temporal fovea (when one is present) which is used in the state of relaxation for convergence upon near objects (Figs. 773-6).

While this is the most generally accepted explanation of teleostean accommodation, an entirely different view has been put forward by Bourguignon and Verrier (1930). Beer (1894) had found that on electric stimulation the campanular muscle contracted and pulled the lens backwards. The former authors failed to substantiate this ; on the contrary, on electrical stimulation they found in a number of species (the roach, the tench, the goldfish, the barbel and the chub) that a deformation of the globe was produced by the tensor choroideæ muscle which encircles the eye at the corneo-scleral junction, resulting in a lengthening of the antero-posterior axis. If the average teleostean eye is hypermetropic ² a retraction of the lens would, of course, increase the optical error and have the reverse of an accommodating effect ; the myopia induced by an increase in the antero-posterior axis would be effective in accommodating for near vision. On the other hand, if, as Beer claimed, the normal refraction is myopic, a retraction of the lens would ensure good distance vision at the expenditure of muscular effort. Further experimental exploration of this mechanism in teleostean fish is required to clear up the position but it is to be remembered that with the spherical lens and its dense central core,

¹ p. 302. Seen also in a well-developed form in tubular eyes with their enormous lenses (Fig. 380).

² p. 638.

the depth of focus of the eyes of Fishes is so great as not to demand much from accommodation.

In Holosteans the lens is slung on a dorsal suspensory ligament and an ectodermal lenticular muscle is present apparently analogous to the campanula ; its action, however, is unknown.

(iii) *A forward movement of the lens*, rendering the eye more myopic to accommodate for near objects is brought about by two separate mechanisms in the vertebrate phylum—by the direct action of a special muscle in Selachians (and possibly Holocephalians) and Amphibians, and indirectly by increasing the pressure in the vitreous cavity as a result of contraction of the sphincter of the pupil, a mechanism seen in snakes.

In SELACHIANS the lens is suspended as in Teleosteans by a dorsal suspensory ligament, and is said to be swung forwards by the action of the smooth (ectodermal) muscle fibres in the ventral ciliary papilla¹ (Fig. 777). Among Selachians, Franz (1905-31) demonstrated such a movement in the rays, *Raja asterias*, and *Torpedo*, doubtfully in the dogfish, *Scyllium*, but not in the dogfish, *Mustelus* ; in some species he found a wide range of accommodation (15 to 20 D). It is to be remembered, however, that neither Beer (1894) nor v. Hess (1912) obtained any such response to electrical stimulation, while Verrier (1930) and Rochon-Duvigneaud (1943) found that the muscular fibres in the ciliary papilla were scanty or absent ; these workers therefore concluded that the accommodation of the Selachians which they investigated was minimal or lacking.

In those AMPHIBIANS which have accommodation, the amplitude is much poorer—never more than 4 or 5 D (Beer, 1898)—an amount quite useless in maintaining good visual acuity in both an aerial and an aquatic environment. Our knowledge of this subject, however, is again meagre and somewhat conflicting. Beer (1898) advanced the theory that accommodation for near vision was attained through the contraction of the ciliary muscles compressing the vitreous body which in turn thrust forwards the lens. His experimental techniques and conclusions, however, have been challenged, particularly by v. Hess (1912) on the basis of his findings with direct electrical stimulation. It is true that in the small eyes of Amphibians with their short focal distance, the length of the receptor elements would allow the image

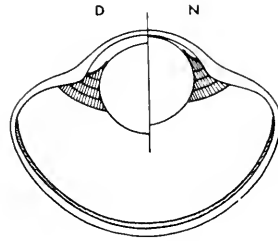


FIG. 777.—ACCOMMODATION IN SELACHIANS.

The eye in the normal condition of rest (*D*, distance vision). The eye in accommodation for near vision (*N*) with the lens moved forwards.

¹ p. 285.

of objects at a considerable range of distances from the eye to fall upon the visual layer so that an efficient and active mechanism may not be required. But it would seem that in ANURANS the lens is pulled forward indirectly by two protractor lentis muscles, a dorsal and a ventral. Unlike the analogous muscles of Fishes, they are mesodermal in origin although still smooth in type. They arise at the margin of the cornea, traverse the iris and are inserted into the large median ciliary processes; these they pull forwards thus drawing the lens in the same direction through its anchorage by the zonule. In URODELES a single ventral protractor lentis muscle inserted into the single mid-ventral ciliary process acts similarly, and less effectively.

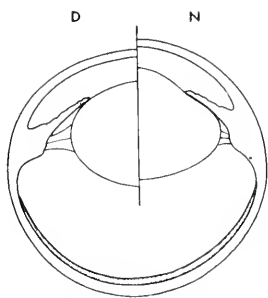


FIG. 778.—ACCOMMODATION IN SNAKES.

The eye in relaxation for distance vision, *D*; the condition in accommodation for near vision, *N*. Note that both the lens and the cornea have moved forward.

the constriction in the circumference of the globe in the ciliary region may be compensated by a slight forward bulging of the cornea. Beer (1898) demonstrated this indirect pressure-effect through the vitreous by removing the posterior half of the globe; electrical stimulation of the ciliary muscle then led to a backward displacement of the lens. In the intact eye an accommodative range sufficient to overcome their +8 or +10 D of hypermetropia is readily available to snakes (up to -17 D) (Kahmann, 1932). The mechanism resembles that seen in Cephalopods.¹

In tree-snakes with a horizontal slit-shaped pupil, a nasal aphakic area and a temporal fovea² the lens moves nasally as well as forwards; this has the optical effect of directing incident light upon the fovea and corresponds to the nasal movement of the lens of those teleostean Fishes with a partially aphakic pupil when accommodation is relaxed for near objects.³

In terrestrial snakes the main effector of the accommodative effort is the mesodermal sphincter at the root of the iris; the action of the

¹ p. 590.

² p. 388.

³ p. 304.

remaining musculature of the iris is insignificant and the relatively firm lens is pushed forwards with little or no change in shape. In water-snakes a supplementary mechanism exists, for in the transference from aquatic to aerial vision such an animal requires an immense range of accommodation. In the European water-snake, *Natrix* (*Tropidonotus*) *tessellatus*, Beer (1898) found that the lens was unusually soft and readily mouldable, and it would appear that in accommodation the powerful sphincter muscle of the pupil moulds the anterior surface into a conical shape as it is thrust forward through the pupil—a mechanism common to other reptiles, particularly the turtle (Figs. 783–5).¹ In this case the lens is thus both displaced and deformed. Aquatic snakes such as the marine cobras (*Hydrophinae*) and river snakes (*Homalopsinae*), as we have seen, make use of a stenopœic pupil when the eyes are out of water to achieve the necessary accommodation, a device also seen in the seals.²

(b) *A deformation of the lens* may be effected by direct muscular pressure upon it or by alteration in the tension of an elastic capsule.

(i) *A direct squeezing of the periphery of the lens by the ciliary body* is a mechanism peculiar to Sauropsidans (except snakes); it is an entirely original and very effective method adopted by this composite group bearing no resemblance to the accommodative devices seen in Fishes or Amphibians. For this reason a number of novel anatomical features is introduced into the sauropsidan eye by virtue of which a high degree of accommodative efficiency is reached. It is significant that the smooth muscle fibres of the Ichthyopsida give place to striated fibres in Sauropsida and a large muscle-mass is developed divided sometimes into two, sometimes three functional segments. Actual contact between the lens and the ciliary body is, of course, necessary; for this purpose a large annular pad has been developed at the periphery of the lens extending it equatorially, and the ciliary body, provided with well-developed ciliary processes, is pushed axially by a deep corneo-scleral sulcus, the deformation of the globe being maintained by a concave ring of dove-tailed ossicles (lacking only in Crocodilians—and snakes). In addition, in order to facilitate its deformation the lens itself is unusually soft so that it is readily mouldable (Figs. 779 to 782).

The optical mechanism of accommodation depends essentially on a deformation of the lens: squeezed laterally by the ciliary processes, steadied posteriorly by the vitreous body, and with the peripheral part of the anterior surface restrained by the contraction of the musculature of the iris, the central area of the anterior surface is bulged forwards in a lenticonus thus increasing the refractivity of the lens and accom-

¹ p. 652.

² p. 641.

modating for near vision. At the same time in lizards and Birds the deepening of the corneo-scleral surface deforms the cornea, producing a peripheral flattening and making it more convex at the apex and thus augmenting the increase in total refractivity (Kahmann, 1932-33); this mechanism is absent in diving birds in which it would be ineffective since the corneal refraction is eliminated under water.¹ The entire

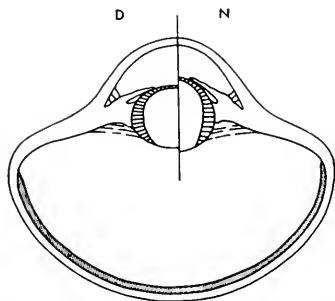


FIG. 779.—ACCOMMODATION IN SAUROPSIDA.

The condition of relaxation for distance vision, *D*, and accommodation for near vision, *N*.

FIGS. 780 TO 782.—TO ILLUSTRATE THE EFFECT OF THE ANNULAR PAD IN TRANSMITTING AN EVENLY DISTRIBUTED PRESSURE TO THE LENS BY THE CILIARY BODY.



FIG. 780.

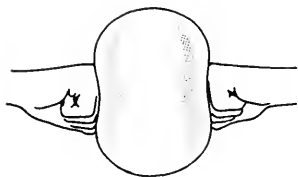


FIG. 781.

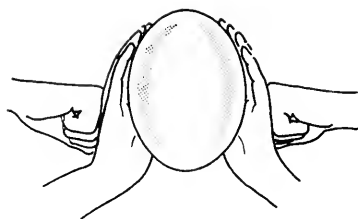


FIG. 782.

Fig. 780, represents a balloon filled with air. If it is compressed directly by a relatively small body such as the fist it is deformed (Fig. 781); if, however, the impact of the fist is distributed regularly by means of an open hand, a lenticular shape is ensured (Fig. 782).

process depends on lateral pressure by the ciliary musculature and pressure from the vitreous plays no active role apart from restraining any change in the posterior surface of the lens: in contrast to the events in the eye of the snake, the process takes place without change if the posterior segment of the eye is removed and the vitreous is eliminated (v. Hess, 1912).

The factor determining the act of accommodation is essentially the ciliary muscle—a well-developed striated muscle running meridionally, a descendant from the minute tensor choroideae of Fishes, but inserted not into the choroid

¹ p. 276.

but into the ciliary body itself. In most Reptiles it is a simple strip running from the corneal margin to the base-plate of the orbicular zone of the ciliary body, but in lizards and in Birds (except diving birds) it is divided into two—the anterior part, Crampton's muscle, strung like a bow-string running between the periphery of the cornea and the sclera, presumably deforms the cornea; the posterior section, Brücke's muscle, thrusts the ciliary body axially on contraction (Fig. 499). In some Birds, Brücke's muscle is still further subdivided, its anterior portion being known as Müller's muscle.¹

A further muscle is seen in Chelonians and lizards—and in (?) the pigeon, *Columba*: the transversalis muscle, a strip of striated muscle originating ventrally in the connective tissue between the ciliary body and the sclera and inserted into the zonular fibres. Its action is to pull the lens nasally thus helping binocular vision on accommodation and convergence. In a sense it seems comparable to the ventral protractor lentis of Amphibians although not homologous with it, and is concerned with binocular vision rather than with accommodation. Such a nasal movement is also aided, particularly in Birds, by the asymmetry of the ciliary body and the anterior segment of the globe.

CHELONIANS have the softest and most readily mouldable lenses amongst all Vertebrates; accommodation in these animals is effected by the formation of an anterior lenticonus by the action of the powerful sphincter pupillæ (Beer, 1898; v. Pflugk, 1908; v. Hess, 1909–12); in these reptiles the annular pad is therefore small and in tortoises and terrapins the ciliary musculature relatively weak (Figs. 783–5). Sea-turtles have little use for accommodation but the undoubted prowess of terrestrial forms in catching insects demonstrates that their range of accommodation must be good.

The accommodation of CROCODILIANS has not been thoroughly explored; Abelsdorff (1898), however, concluded that it extended to a range of 8 D. Similarly *Sphenodon* with its weak ciliary muscle can only accommodate little—if at all; the greatest effect would seem probably, as in turtles, to come from the deforming effect of the sphincter of the iris on the anterior surface of the lens.

LIZARDS, on the other hand, have good accommodation, their excellent mechanism being aided in some cases (nocturnal geckos) by the stenopœic contracted pupil. Electrical stimulation has been found to increase the refraction considerably—by 15 D in *Iguana*, 10 D in *Lacerta* (v. Hess, 1909–12).

In BIRDS the accommodative mechanism is superb, the most efficient, indeed, amongst Vertebrates, and in these, as in turtles, the formation of an anterior lenticonus is aided considerably by the powerful contraction of the sphincter muscle of the pupil which acts as a "compressor lentis" (v. Hess, 1910–12). In the owl, *Bubo*, the range is small (probably some 4 D), in the nocturnal predators, 2 to 3 D and exceptionally 4 D, in the average passerine bird some 8 to 12 D, and in the predatory birds (hawks, eagles, etc.) still greater. The highest

¹ p. 406.

range is seen in aquatic birds such as the cormorant, *Phalacrocorax*; in it the lens is very soft and plastic, the sphincter of the iris extremely powerful, and the compression and moulding of the lens to form a marked lenticonus has been said to provide an accommodative excursion of up to 50 D in vision under water (v. Hess, 1912).

FIGS. 783 TO 785.—ACCOMMODATION IN CHELONIANS.

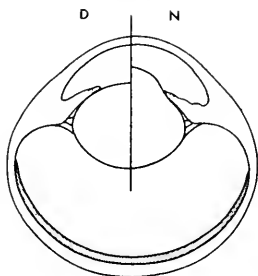


FIG. 783.

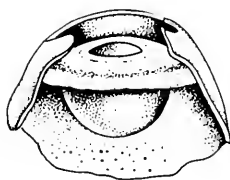


FIG. 784.

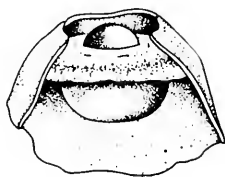


FIG. 785.

The lens at rest for distance vision (*D*, Fig. 783 ; Fig. 784) ; deformed into an anterior lenticonus for near vision (*N*, Fig. 783 ; Fig. 785).

(ii) *A deformation of the lens by a variation in the elasticity of the capsule* is a mechanism peculiar to MAMMALS and has no analogy elsewhere in the vertebrate phylum. According to the most generally accepted hypothesis of Helmholtz (1855) and Fincham (1925), the plastic lens retains its characteristically flattened shape owing to the moulding effect of the elastic capsule stretched by the pull of the zonule. The capsule varies considerably in thickness, being thinnest at the posterior and anterior poles. When the ciliary muscle contracts on accommodation, the ciliary body approaches the lens, the zonule slackens and the capsule relaxes allowing the plastic lens to assume a more spherical shape—the shape, in fact, which it assumes when removed from the eye. Since the posterior pole is restrained by the support of the vitreous body and the capsule is relatively thick and tough in the peripheral region, the greatest bulging occurs in the form of a conus-

like projection on the anterior surface, thus increasing its refractivity in accommodation for near objects (Figs. 786 to 790).

Compared with the sauropsidan plan, such a mechanism is inefficient; with a large lens much deformation cannot occur, and if the lens loses its plasticity any deformation is impossible. In a small eye with a large lens accommodation is therefore negligible and when the

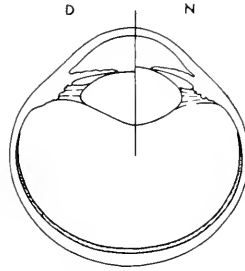


FIG. 786.—ACCOMMODATION IN MAMMALS.

The condition of relaxation for distance vision, *D*; and accommodation for near vision, *N*.

FIGS. 787 TO 790.—THE LENS CAPSULE IN MAMMALS.

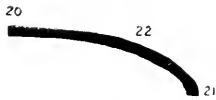


FIG. 787.—Rabbit.

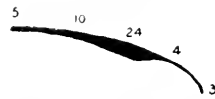


FIG. 788.—Capuchin monkey.

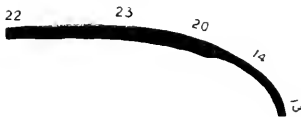


FIG. 789.—Sheep.

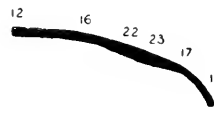


FIG. 790.—Man.

Diagrams, in which the thickness of the capsule is greatly magnified, showing the relative thicknesses in different regions (E. F. Fincham).

lens becomes sclerosed with age (as in man) it gradually fails. On the whole the efficiency of mammalian accommodation is therefore poor. In most of the lower Mammals the ciliary muscle is vestigial and sometimes absent: the more primitive Mammals have therefore no accommodation. Among RODENTS, accommodation is known only among squirrels (*Sciuridæ*) and in them the range is insignificant (1 to 1.5 D). No UNGULATE appears to have any accommodation, and the range in CARNIVORES is small (1 to 3.5 D)¹ with the exception of the otter,

¹ The range of accommodation in the dog has been reported as 1.0 D, in the wolf as 2.75 D (v. Hess and Heine, 1898), in the cat as varying from 1.75 D (v. Hess and Heine, 1898) to 3 D (Marg *et al.*, 1934-5) or 3.5 D (Hartridge and Yamado, 1922).

Lutra ; this animal has a well-developed ciliary muscle and, in addition, a powerful sphincter of the iris which appears to aid the deformation of the lens after the manner of Sauropsidans so that its accommodative range can cope with vision in air and also under water. In air the animal is emmetropic and under water its visual acuity is sufficiently good to allow it to capture its prey with considerable agility. PRIMATES as a class possess the most effective range before senescence sets in (up to 10 D in the ape ; up to 20 D in the human infant, decreasing to 10 D at 21 years, thereafter rapidly diminishing).

A résumé of the occurrence and configuration of the ciliary musculature may be useful at this stage. It is, of course, absent when the ciliary body as such is absent or reduced to a flat ciliary zone (Cyclostomes, the coelacanth, Dipnoans, Chondrosteans and Caecilians) ; it is also absent in Monotremes and is vestigial in Rodents, Insectivora and Sirenia. The muscle is plain in Fishes, Amphibians and Mammals ; striated in Reptiles and Birds. It is represented by a small TENSOR CHOROIDEÆ in Teleosts and Amphibians (discontinuous in two strips above and below). This becomes a CILIARY MUSCLE in Reptiles, Birds and Mammals. Accessory musculature is represented by a PROTRACTOR LENTIS in Selachians (ectodermal) and Amphibians except Caecilians (mesodermal ; dorsal and ventral in Anurans, ventral in Urodeles) ; a RETRACTOR LENTIS is present in Teleosts (except eels) and Holo-steans. A TRANSVERSALIS MUSCLE is found in Chelonians, lizards, (?) *Sphenodon* and (?) the pigeon. The segmentation of the ciliary muscle into Crampton's and Brücke's muscle in most Reptiles and, in addition, into Müller's muscle in Birds has already been noted. In snakes the ciliary muscle has migrated to the iris.

Among all the activities of Vertebrates, the needs of the *amphibious animal* which requires to see both under water and in the air put the greatest strain upon accommodation, a circumstance which applies both to fish which emerge into the air and to land animals which go down into the water. The elimination of the corneal refraction when it is immersed in water and its optical value in air make the same eye strongly hypermetropic in the first medium and strongly myopic in the second. So difficult is this optical transition that it is not attempted by many forms. Thus certain fishes such as the climbing perch, *Anabas*, which emerges on land crawling with the aid of the spines on the gill-covers and on the anal fin, may be without effective accommodation or any other detectable device for altering their relatively emmetropic state in water ; in these vision in air must be so myopic as to serve merely for the detection of light and shadow. Other fish such as the Indian mullet, *Mugil corsula*, have eyes of the type designed for aerial vision with a lenticular-shaped lens ; this fish swims feeding on the surface with the eyes out of water and its visual acuity beneath the water must be relatively poor, a consideration which applies also to such semi-aquatic animals as the ranid frogs, the crocodiles and the hippopotamus. Conversely, the penguins (unlike most other birds) are very myopic in air ; while Sirenians, without accommodation and with a slight myopia in air, appear to have so little visual acuity in either medium that vision can play only a small part in their activities.

Where the attempt is made to bridge over the optical transition demanded by vision in two media, this may be accomplished in several ways. In the first

place, a superlative degree of accommodation may be provided. This is seen in a fish such as the mud-skipper, *Periophthalmus*, which can become emmetropic in air using a maximal degree of accommodation. Among land animals a similar excellent accommodation may allow the neutralization of the hypermetropia which supervenes on immersion. This applies mainly to representatives of the Sauropsida which employ a well-developed ciliary muscle together with a hypertrophied sphincter muscle of the iris to mould an unusually soft lens—turtles, water-snakes and birds such as the cormorant. One Carnivore, the otter, *Lutra*, is capable of a similar accomplishment.

Apart from this exceptionally high degree of accommodation, several adaptive expedients which we have already mentioned, all of them both interesting and ingenious, may be summarized :

(a) The provision of two optical systems by the use of one or other of the two main axes of a pyriform lens as is seen in *Anableps* with its two pupils, or in the kingfisher, *Alcedo*, with its two foveæ.¹

(b) Contraction of the pupil either to a stenopœic opening, as is seen in the sea-snakes (Hydrophinæ) or a stenopœic slit, as in the seals (Phocidæ).²

(c) The incorporation of the nictitating membrane into the optical system when the eye is immersed, as in diving ducks, loons and auks.³

Other optical factors. Apart from the refractive error and its susceptibility to adjustment, the sharpness of the retinal image is influenced by other optical factors. One of the most important of these is the size of the eye, a consideration which essentially determines the size of the image, and therefore the degree of its resolution ; since the size of the visual elements is relatively constant, a larger image stimulates more of them, thus allowing a finer analysis. On the whole, therefore, those animals with relatively large eyes, such as Birds, have the higher visual acuity. In the same way, a flattening of the lens and an approach of this tissue towards the cornea increase the distance between the nodal point of the dioptric system and the retina and again increase the size of the image (Figs. 747-8) ; this expedient is well seen in the eyes of Birds and Primates. The small anterior segment with the forward position of the lens and the large globular posterior segment so typical of diurnal birds are excellent examples of this adaptation (Fig. 749). Finally, an efficient pupillary stop to eliminate aberrations by the peripheral part of the lens is of value in increasing the resolution of the image so long as excessive contraction does not diminish the visual acuity by cutting down too drastically the entering light.

It is to be noted that when the lens is spherical, the aberrations developed in the periphery are less important. This is seen particularly in Fishes in which the refraction of the cornea is eliminated, the lens is spherical with a graduated index of refraction, and the retina practically concentric with the lens (Matthiessen, 1886-93). In such an eye the optical system is practically aplanatic and panoramic, and a pupillary stop is not needed—and is seldom provided.

¹ p. 641.

² p. 641.

³ p. 643.

A specific device developed by certain species in order to increase the visual acuity is the provision of INTRA-OCULAR FILTERS. These increase the sharpness of the image in the same way as tinted spectacles do when appropriately chosen: they diminish chromatic aberration largely by eliminating some of the blue and most of the violet rays, while at the same time they cut down the glare and dazzle caused by irregularly scattered light from a bright sky. As would be expected this device is largely confined to diurnal Vertebrates and is not typical of nocturnal types to which the transmission of every available ray is of importance (Walls and Judd, 1933).

For these optical purposes a yellow filter is the most efficient and is the most widespread optical device found in the vertebrate eye. Thus a yellow cornea is found among Holosteans in *Amia*, and in a few highly diurnal Teleosts such as the carp, *Cyprinus*, and the pike, *Esox*; a yellow lens is found in the lampreys (except the nocturnal *Geotria*), in the diurnal gecko, *Lygodactylus*, in some diurnal snakes (*Malpolon*, *Dryophis*, etc.), in the tree-shrew, *Tupaia*, among Insectivores, and in most squirrels (Sciuridæ, except the nocturnal flying squirrels); a yellow pigment is found in the central area of the retina, possibly in the chameleon and certainly in man, converting it into a macula lutea; and yellow oil-droplets are found in the cones of the frog, *Sphenodon*, the turtles, diurnal lizards and birds. Finally, as was originally pointed out by Schultze (1867), the blood in the capillaries in the membrana vasculosa retinae of Holosteans, many Teleosts,¹ Anurans and snakes, and in the vascularized retina of the eel and some Mammals² must constitute an effective yellow filter through which light must pass to reach the cones.

We have seen that orange and red and occasionally green droplets in addition to yellow, occur in the cones in the periphery of the retinae of turtles and diurnal birds; these must aid visual discrimination by enhancing colour-contrasts.³

THE STRUCTURE OF THE RETINA

Not only does the visual acuity depend on the efficiency of the dioptric system of the eye, but also—and equally—on the ability of the retina to act as an analytical receptor. This ability depends essentially on two factors—the fineness of the mosaic of retinal receptors and the degree of summation in this tissue.

If the simplest pattern of two object-points is to be analysed, each must stimulate a separate receptor element while an intervening element must remain unstimulated. So far as the retinal mosaic is concerned, therefore, the greater the number of visual cells and the closer their packing, particularly in the important receptor area of the

¹ p. 299.

² p. 479.

³ p. 631.

retina, the higher will be the acuity. For this reason the potential visual acuity of the tiger-snake, *Notechis*, with its immensely bulky cones, or of some deep-sea Teleosteans (as the pike-perch, *Stizostedion*) in which the visual cells are so large that the retinal mosaic can be seen ophthalmoscopically (Figs. 345, 348), is necessarily much inferior to that of the chameleon which has 756,000 visual cells per sq. mm. at the fovea, or the hawk, *Buteo*, which is said to have a foveal density of 1,000,000 cones per sq. mm. (Rochon-Duvigneaud, 1933). In this respect the sauropsidan retina, particularly that of lizards and birds, is supreme, and considerably more effective than that of any mammal: the cone population at the human fovea is approximately 200,000 per sq. mm.

In order to promote visual acuity a specialized AREA CENTRALIS is frequently developed wherein the receptor elements are more closely packed than elsewhere in the retina. Such an area, as we have seen, is found in varying states of differentiation in representatives of most of the classes of Vertebrates and is characteristic of diurnal types. It is absent in the primitive Cyclostomes, in Selachians except the dogfish, *Mustelus*, in the coelacanth, Chondrosteans, Holosteans, in Urodeles, in nocturnal lizards and snakes, and in Mammals except some Rodents particularly the squirrel family (Sciuridae), the Ungulates, Carnivores and Primates. In location such an area may be central or temporal; in shape, rounded, band-like or (exceptionally) crescentic or ring-shaped (Anurans); it is usually single but sometimes is duplicated. In it the visual elements have become slender and closely packed, an increase in receptor elements which involves a corresponding increase in the number of bipolar and ganglion cells in the retina and therefore in the thickness of this tissue.

The following are provided with an area centralis (macula) without a fovea: dogfish, *Mustelus* (central and round), most Teleosteans (mainly temporal in location, except in *Hippocampus* where it is central), Anurans (crescentic in shape over the optic papilla), Crocodilians (horizontal band), Chelonians (central, round), rabbits and squirrels (ill-defined, horizontal band), Ungulates (sometimes a broad horizontal band, usually temporal, sometimes a temporal round area, sometimes a combination of both), most Carnivores (well-defined and central), nocturnal Prosimians and *Nyctipithecus* (central and round). Two teleostean fishes have two areas without a fovea, the killifish, *Fundulus*, with two ventro-temporal horizontal ridges, and the guppy, *Lebistes*, with an axial and a ventral area.

There is evidence that the area centralis in certain species acts as a device to increase sensitivity rather than acuity, the visual elements, mainly rods, being multiplied for this purpose.¹ This is seen particularly in nocturnal, or, at any rate, not strictly diurnal types—the Crocodilians, the echidna, the opossum, and perhaps most Ungulates and some Carnivores. Such a function would certainly seem to apply to the pure-rod foveae of the deep-sea teleost, *Bathytroctes*, of the gecko, *Sphaerodactylus parkeri*, and of *Sphenodon*.

¹ p. 673.

A further device for increasing the resolving power is the development of an excavated FOVEA within the central area. The classical view of the rationale of this pit-like configuration is that the outspreading of the cellular layers of the retina and the consequent thinning of this tissue in the central pit reduce the absorption and scattering of the light as it traverses the retinal layers to reach the receptor cells. It is questionable, however, if the retinal tissue is much less transparent than the vitreous and it seems probable that in well-developed foveæ at any rate, a refractive magnification of the image is a more important optical effect (Walls, 1937). It was shown by Valentin (1879) that the refractive index of the retina is considerably higher than that of the vitreous; this being the case, incident light will be diverged as it strikes the curved sides of the pit (Fig. 791).

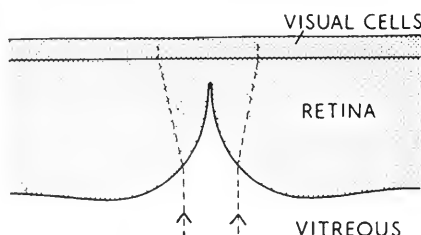


FIG. 791.—THE MAGNIFYING EFFECT OF THE FOVEA.

Owing to the fact that the index of refraction of the retina is higher than that of the vitreous, incident light striking the clivus of the foveal depression is refracted laterally so that the image is magnified.

This theory, advanced by Walls (1937), demands that the most efficient fovea will have a deep pit with highly convex sides, and this is indeed the case; in Birds, for example, the linear magnification thus obtained is of the order of 13% and the areal magnification, 30%. As Walls puts it, when the area centralis has done everything possible to increase the number of receptor units over which an image will fall, a further increase in efficiency is gained optically by the magnification of the image. A shallow or broad fovea thus probably acts by eliminating the dispersion of light as it traverses the retina, a deep well-formed fovea with a steeply curving clivus acts also as an effective magnifying device (Figs. 792-5).

A further and equally interesting function for the fovea has been suggested by Pumphrey (1948). From the optical point of view he reasoned that a deep convex-clivate fovea would produce a distorted image peripherally and a clear image only at the centre of the depression; the shape of fovea could thus be interpreted as a mechanism to maintain accurate fixation of the eye and might be used to appreciate in exaggerated form the angular movements of objects which are being fixated. This function, of course, would be attained at the

expense of the visual acuity. Pumphrey therefore suggested that foveæ developed along two possible lines—one, the shallow fovea towards greater acuity as in man, and the other, the convex-clivate fovea for the purposes of rapid alignment of the fixation object, as in birds of prey.

A relatively inefficient fovea of the first type is seen in a number of Teleosts,¹ in *Sphenodon*, in *Amyda* among the turtles, in two types of tree-snake,² in most ground-feeding and domesticated and many nocturnal birds, in the temporal fovea of bifoveate birds (except the eagle), in *Tarsius* and the Simians. A deep fovea combining tenuity of the retina with magnification of the image is seen in its highest form in lizards, in the central fovea of predatory birds, in the temporal foveæ of the eagle and the swift, *Micropus*, and in the marmoset, *Hapale*. In some water-birds (gulls, shearwater, flamingo) the fovea is horizontally oval and trough-like.



Swift

FIGS. 792 TO 795.—THE SHAPE OF THE FOVEA.

FIG. 792.—*Sphenodon*.

FIG. 793.—A primate.

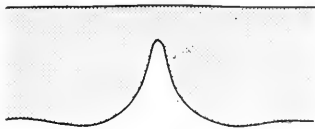


FIG. 794.—The chameleon.

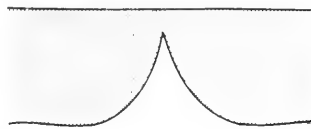


FIG. 795.—A hawk.

In its position the fovea is usually central, subserving lateral vision when the eyes are so placed, and binocular vision when the visual axes are frontally directed. A temporal fovea, situated far out in the periphery of the retina, subserving forward vision with laterally placed eyes, is found in Teleosts, the foveate snakes, in the owl and bifoveate birds; only in wing-feeding passerine and predatory birds, and in the arboreally active lizard, *Anolis*, are two foveæ found, a central for unocular vision and a temporal for binocular vision.³

In the structural basis for visual acuity the degree of summation in the retina, that is, the number of visual elements connected to a single optic nerve fibre, is a factor as important as the density of the retinal mosaic. In general, in the interests of sensitivity⁴ many rods are associated with a single ganglion cell; in the interests of acuity in ideal circumstances each cone would relay through a bipolar cell to an individual ganglion cell, the impulse from which would be relayed to the brain by a separate nerve-fibre. Each visual element would thus have



Flamingo

*Anolis*¹ p. 309.³ See further p. 684.² p. 388.⁴ p. 609.

a "private telephone wire" to the brain, so that each cone would make its individual contribution to the resolution of a pattern. In an eye designed to attain a high visual acuity, therefore, the retina is rich in cones, its area of special differentiation or fovea is pure-cone, the inner nuclear layer is thickly packed and composed of many layers of cells and the ganglion cells are necessarily numerous (Fig. 756); in such a retina there is thus little summation and the ratio between the optic nerve fibres and receptors is high.

Thus Franz (1934) estimated that the great summation in the retina of Selachians (visual cells 10,800/sq. mm., ganglion cells 1,500) must reduce their visual acuity to 5% of that of man (200,000 : 200,000 in the central fovea), while, also owing to its high summation, the resolving power of the eye of the whale can be only 2% of that of man.

The remarkable superiority of the retina of Birds is shown not only in the regularity of the arrangement of the cells but in their numbers, so that the ratio of conductive to sensory cells is exceptionally high. In the American "robin", *Turdus migratorius*, for example, cellular counts outside the foveal region give the astonishing figures of: outer nuclei, 3 rows of cells; inner nuclei, 28; ganglion cells, 3 (Walls, 1942). Even in the week-old chick the corresponding figures for the peripheral retina are: 2.5, 18, 2.5. Similarly in the peripheral retina of the white wagtail, *Motacilla alba*, there are 120,000 visual cells per sq. mm. with a corresponding 100,000 ganglion cells; in the fovea of the English sparrow, *Passer domesticus*, 400,000 (Franz, 1934), and in the hawk, *Buteo*, 1,000,000 (Rochon-Duvigneaud, 1943). In the human fovea the corresponding figure is 200,000. Even in the peripheral retina of the nocturnal owl, *Bubo*, there are 56,000 visual elements per sq. mm. summing 3,600 ganglion cells, while the overall summation ratio of the human retina is 125 : 1 (Walls, 1942). In the comparative disability of daylight the owl would thus appear to have a potential visual acuity greater than man, while the resolving power of the peripheral retina of the hawk should be twice, and that of its fovea eight times that of the human fovea.



Motacilla



Hawk, *Buteo*

THE VISUAL ACUITY OF VERTEBRATES

Among FISHES the general acuity is probably relatively poor (v. Hess, 1909-14), but among some Teleosts the complexity of the retina and the provision of a fovea indicate the possibility of a relatively high grade of resolution. Training experiments depending on the discrimination of form in a number of Teleosts have furnished interesting results. Goldsmith (1914) and Maes (1930) found that goldfish were adept at this, while Rowley (1934) established that they could distinguish between circles held in front of them the diameters of which differed by only 3 millimetres; Herter (1929-53) trained minnows to differentiate between circles, squares, triangles and crosses; and Meesters (1940) obtained similar results with sticklebacks with curved figures. It is obvious from the experiences of deep-sea divers such as Beebe (1934) and Cousteau (1953) that certain fish, at any rate, exhibit a degree of curiosity regarding strange elements in their



Minnow



Stickleback

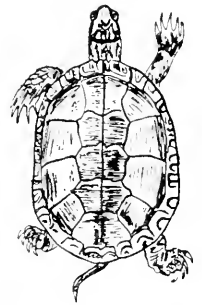
environment which can only be explained by the possession of a considerable degree of form vision and sufficient appreciation of the meaning of objects to influence their ordinary activities.

Some AMPHIBIANS, such as the frog and toad, are essentially visual animals; they catch their insect food with great dexterity, a feat demanding considerable visual acuity, and recognize their mate by sight several inches away (Banta, 1914). Moreover, there is some evidence from their homing ability and capacity to recognize their territory that their behaviour is determined to some extent by visual memory although other senses undoubtedly contribute, sometimes to a preponderant degree (Breder, 1925, in *Hyla*; Czeloth, 1930, in *Triturus*). The inertia and lack of intelligence of Amphibians, however, make experimental exploration of their form-sense difficult. On the whole it would appear to be defective: in this respect they are much inferior to fishes. Thus frogs have been found to be unable to distinguish between a lighted space and a white solid; trained to the former they would attempt to struggle into a solid white surface (Dickerson, 1906); but Pache (1932) was able to train *Hyla* to distinguish between a triangle and a circle. It would seem that movement-sight plays a much greater part than form-sight in their visual activity both in natural surroundings and experimental training.

Among REPTILES a high acuity of vision is seen only among lizards and to a less extent among turtles. We would expect the excellent fovea of lizards to provide a correspondingly good visual acuity, an expectation borne out by the accuracy of their fly-catching: the unerring aim of the long tongue of the chameleon is proverbial.¹ With their cone-rich retinae the same applies to Chelonians; thus a turtle will deftly catch an insect in flight and a domesticated specimen is said to recognize the person who feeds it at a distance of 50 metres while paying no attention to a stranger (Rollinat, 1936). Moreover, in training experiments turtles have been found to be able to distinguish between such forms as horizontal and vertical lines, circles, triangles and squares or other simple geometrical figures (Casteel, 1911; Parker, 1922; Kuroda, 1933; Wojtusiak, 1933; Myluarski, 1951). It would thus seem that these animals have a relatively high capacity for form vision. On the other hand, the comparatively crude nocturnal retinae of the Crocodilians and of *Sphenodon* necessitate a low acuity. Among the Ophidians the tree-snakes and bird-snakes provided with a fovea² and binocular vision³ are the only species which depend essentially on their eyes in striking their prey; but the visual acuity of snakes as a class is probably the lowest among all diurnal Vertebrates, much more dependence being placed on other senses such as smell and touch.⁴

*Hyla**Triturus* (male)

Chameleon



Turtle

¹ p. 695.² p. 388.³ p. 674.⁴ p. 599.

The highest visual acuity in the entire vertebrate phylum is seen in BIRDS ; this we would expect with their enormously large eyes with an anteriorly placed lens and a globular posterior segment, their emmetropic refractive condition and magnificent accommodative mechanism, the multiplicity of oil-droplets in the cones, the excellence of their foveæ, the perfection of the lamination and the low summation of their retina. This is indeed the case, for the visual resolution attained by some of the passerine wing-feeders and the predators is phenomenal. Investigating this problem, Pumphrey (1948) estimated that a resolution of about 10'' of arc should be possible by the avian retina, three times the accuracy attainable in the human retina, and in training experiments, Grundlach (1933) actually demonstrated a resolution down to 23'' in pigeons ; in these birds a high degree of form-discrimination can be developed although it tends to be primarily unidimensional (Chard, 1939 ; Towe, 1954 ; Jones, 1954). In this connection it is to be remembered that the degree of resolution capable by a bird such as the hawk ought to be of a considerably higher standard than that of the pigeon.



Pigeon

This potentiality is borne out in the everyday activities of birds (von Hess, 1912 ; van Eck, 1939 ; Rochon-Duvigneaud, 1943 ; Donner, 1951 ; and others). It is true that many insect-catchers such as the swallow or the night-hawk trawl for their food indiscriminately on the wing particularly during the twilight hours with little reliance on vision ; but the visual acuity of the martlet which flies high and at intervals swoops downward upon an individual insect at a considerably lower level, or that of the humming-bird which opens its long narrow beak but slightly and impales minute insects individually with its long bifid tongue, must be superb. In many birds the visual acuity far exceeds that of man ; the reactions of fear by the shrike, *Lanius*, which the falconer carried with him in a cage, let him know the whereabouts of his bird of prey long after he himself had lost track of it in the sky. Even an owl, the eye of which is specialized for night vision,¹ will detect a hawk approaching in the day-sky at a height at which it is invisible to man. The excellence of the optical resolution of which the avian eye is capable is probably aided by a markedly high capacity to differentiate tones, a faculty possibly based on the light-filtering effect of the oil-droplets of their cones² ; thus dead game lying on the ground, to us completely camouflaged by its surroundings, will be seen by the African vulture—and it will recognize that it is dead—from a height of 3,000–4,000 metres, a height so great that a man cannot discern the bird in the sky with its 3-metre wing-span.

Shrike, *Lanius*

¹ See p. 605. It is to be noted that according to v. Hess (1912) the retina of the owl contains 2,500,000 cones.

² p. 631.

This superb acuity is not, of course, universal among birds. Thus, testing the vision of domestic hens to see a grain of wheat in strange surroundings, Engelmann (1952) concluded that the limiting value was determined by a retinal image 0.02 mm. in diameter. Nor is their form sense, despite the excellence of its physical basis, always fully exploited. Conditioning experiments have been undertaken on a considerable scale in birds, particularly the pigeon, a research pioneered by Popov in Pavlov's school (see Razran, 1933) (ten Cate, 1923 ; Beritoff, 1926 ; Riddle and Burns, 1931 ; Towe, 1954 ; Jones, 1954 ; and others). It has been established that birds are eminently trainable to distinguish between different kinds of geometrical figures of equal area, and that the development of their sense of form is relatively high. At the same time, when pigeons are offered a choice of a number of visual variables in discriminative problems they always respond consistently to one of the variables only. Jones (1954) established that cues based on colour were most readily followed, those depending on position came next, while form discrimination was the most difficult to learn.

The excellence of the form perception of birds is also seen in their extraordinary powers of recognition. This is a well-attested phenomenon ; birds rapidly learn to recognize each other even when two weeks old (the coot, *Fulica*, Alley and Boyd, 1950) and recognition is often made entirely on a visual basis even when the bird in question is silent. Robins (*Erithacus*) can recognize their silent mates at a distance of over 30 yards even although they are partially screened by trees (Lack, 1939) ; tits (*Parus*) can distinguish individuals in a flock at 60 yards distance (Morley, 1942), while pintails (*Dafila*) can identify one another 300 yards away (Hochbaum, 1944). An artificial change of appearance as by transferring the comb to the side of the head, may destroy recognition (see Thorpe, 1956). Recognition of human beings by birds is also well known, the facial characteristics sometimes being recognized in spite of a change of clothing (Poulsen, 1944 ; Buxton, 1946 ; Ash, 1952 ; Thorpe, 1956). In this respect also the visual memory may be long ; it is true that in some species impressions may fade after a few days, but jackdaws can remember individuals for several months (Lorenz, 1935), a pigeon has been said to remember a particular person after 11 months (Diebschlag, 1940), and a hen trained to eat off a certain colour performed her task again a year after the training had ceased (Claparède, 1926). The annual return of many migratory birds to the same spot is another case in point.

Most MAMMALS are in an entirely different category ; only the Sciuridae (the entire retina of which may be said to be a macula), a few Carnivores, some Ungulates, and Primates have a highly developed visual acuity. Thus in rats and mice training experiments show that



Marmot

form-discrimination is relatively poor (Karli, 1954 ; and others). On the other hand, the care-free agility of the arboreal squirrel necessitates an unusually keen vision, while the marmots in the Alps with their pure-cone retina will whistle as they spot a climber long before he can see them. In dogs, Pavlov (1911-27) found that conditioned reflexes could be developed depending on the discrimination between ellipses and a circle with a differentiation of the semi-axes of only 8:9—a very high standard of efficiency. Among the Ungulates the acuity is higher than would be expected in a rod-rich, afoveate eye, possibly because their eyes are usually large ; the horse or the deer, although

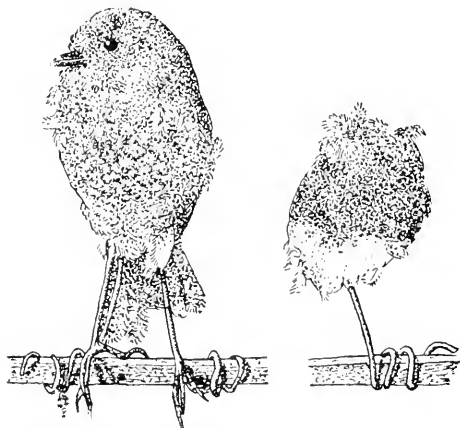


FIG. 796.—THE VISUAL RESPONSES OF THE ROBIN.

On the left is a mounted young robin with a dull brown breast ; on the right a tuft of red feathers. The territory-holding male threatens the bundle of red feathers rather than a complete robin which lacks red feathers (from Lack ; Tinbergen, *Study of Instinct* ; Clarendon Press).

relying largely on movement, has excellent sight, while the acuity of the higher Primates (and man), although not equal to that of Birds, is sufficiently high for vision to become the dominant sense in regulating conduct.

In any appreciation of the visual capacity of animals, however, whether Fishes, Reptiles, Birds, or Mammals, it is to be remembered that their visual perceptions often differ from our own in that they are limited to one or a few relatively simple “ sign-stimuli ” of form, colour or movement, and not to all the visual elements of the situation. For this reason the pattern of innate behaviour can be released by the exhibition of crudely coloured models in which resemblances of form are very inexact. The threat-display in the male robin, for example, is elicited by an isolated bundle of red breast feathers having little resemblance to the bird’s usual rival (Fig. 796) (Lack, 1943), or that of the lizard,

Lacerta viridis, by a crude clay model so long as it has a blue throat (Kitzler, 1941).¹ The feeding reactions of young herring-gulls are initiated by crude models simulating only in a rough and ready manner the red patch on the parents' mandible which forms the normal stimulus (Tinbergen and Perdeck, 1950) ; and despite their remarkable visual acuity birds show incubation responses to objects other than eggs so long as they are small and round (Kirkman, 1937), or exhibit escape reactions to a crude dummy as if it were an enemy bird of prey, no matter what the colour or the shape of its wings and tail may be, so long as the neck is short (Lorenz, 1940). So also will the male stickle-back, *Gasterosteus aculeatus*, react differently to a crude model of a fish : in the head-up position it will exhibit mating activity, in the head-down position it will exhibit fight (Tinbergen, 1948) and it will be similarly stimulated by a truck passing outside its window provided only that it is red as the belly of its natural rival.

The differences between visual acuity in those members of the vertebrate phylum which have been experimentally investigated, and particularly the difference between diurnal and nocturnal animals, are seen in the following figures which refer to minutes of minimum visual angle :

Diurnal—man, 0.44 to 0.83 ; chimpanzee, 0.47 ; rhesus monkey, 0.67 ; cebus monkey, 0.95 ; homing pigeon, 0.38.

Nocturnal—cat, 5.5 ; alligator, 11.0 ; opossum, 11.0 ; rat (pigmented) 26.0, (albinotic) 52.0.

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THE PERCEPTION OF SPACE

An appreciation of space and an ability to localize objects therein are essential requirements of all organisms. It is obvious that any capacity for the exploration of space must be referred to some system

of coordinates. Plant life orientates itself with regard to gravity (geotropism); equally, in animal life the mechanism which maintains the posture of the body—the basis of its perception of space—uses the same fundamental reference-frame, and when a vertebrate is at rest it utilizes an elaborate system of static postural reflexes designed to maintain its equilibrium and provide a starting-point for its contacts with the outside world. These are supplemented by a further system of stato-kinetic reflexes which serve a similar purpose to the animal in motion (Sherrington, 1904-6; Magnus, 1924). It is this combination which maintains the organism right-side-up and allows it to retain its relationships with its environment.

With this mechanism as basis, space is explored egocentrically by the various senses, every one of which contributes in some degree to the common aim. The immediate vicinity can be explored by the tactile sense; but the development of projicient senses is necessary for the appreciation of anything beyond the restricted area which the animal can touch. It is true that the tactile sense can be projected to some extent, as by the appreciation of vibrations as is seen in the ability of snakes to record ground-vibrations through the lower jaw,¹ a facility akin to that displayed by web-spinning and ripple-spiders.² The olfactory sense and to a greater extent the auditory sense act as adjuvants for this purpose, but with the exception of the astonishing development of the auditory powers of bats,³ these form inefficient and unreliable guides. The remarkable thermal sense of certain colubrid snakes⁴ forms another exception; but as a general rule throughout the vertebrate phylum extended spatial judgments, at least in diurnal species, are essentially dependent on vision which makes by far the greatest contribution to the perceptual range of the animal and to the accuracy of its assessments.

Visual spatial perceptions may be classified into two main types each of which may be divided into two attributes:

- (1) Bi-dimensional perceptions, made up of
 - (a) the perception of direction which allows an estimation to be made of the position of an object relative to the body;
 - and (b), an extension of this faculty into the perception of bi-dimensional distance (or extensity) allowing an estimate to be made of the angular extension of an object.
- (2) Tri-dimensional perceptions, made up of
 - (a) the perception of depth which includes the capacity of stereoscopic vision when binocularity is attained;
 - and (b), an extension of this faculty into the perception of size, a psychological appreciation of the size of a body emerging as

¹ p. 599.

³ p. 601.

² p. 579.

⁴ p. 600.

a unitary perception based upon estimates of the extent of the retinal image and its distance away.

Such perceptions depend on a number of physiological and psychological factors. The primary factor in a visual analysis of space is the characteristic of *local sign* in the retinal elements—that innate property, possessed by all distinguishable parts of the body, whereby the excitation of one receptor is discriminated from the excitation of its neighbours, so that all object-points are projected visually with regard to the eye as spatial entities separate from all other points. In

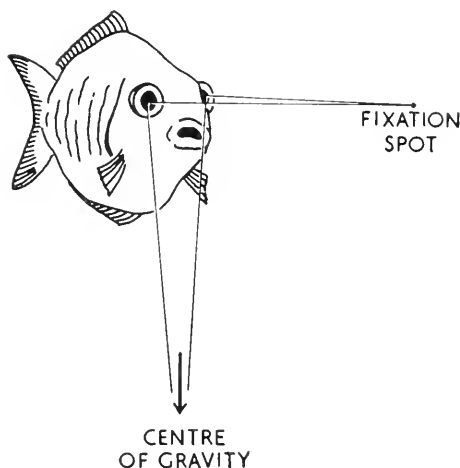


FIG. 797.—THE FRAME OF REFERENCE IN SPACE

The two fundamental coordinates—the vertical determined gravitationally from the earth's centre and the horizontal determined visually from the horizon.

animals possessed of an area centralis or fovea,¹ this region is pre-eminently possessed of local sign and forms the primary point of reference; images formed thereon are projected along a central base line (the fixation line) in relation to which images falling on eccentric retinal points are correspondingly located. Such a mechanism is applicable to each eye separately, but when the visual fields overlap, within the area common to both, sensory impressions are synthesized into a unity so that objects in space are projected along a line of direction emanating from a hypothetical, centrally situated cyclopean eye. It is the simultaneous presentation to consciousness of two slightly dissimilar images in this way that forms the basis of stereoscopic vision. In addition to this retinal mechanism orientating objects in space with reference to the eyes and establishing an *egocentric*

¹ p. 657.

localization, the postural mechanism persists which extends the frame of reference to provide a *gravitational localization* (Fig. 797). Visual perceptions are synthesized with impressions from the extra-ocular muscles, the neck and the labyrinths, so that visual orientations are related to movements of the eyes with respect to the head, of the head in respect to the trunk, and of the trunk in respect to gravity, and thus an exploration of space is attained on a gravitational basis. These fundamental mechanisms on the physiological level are innate and hereditarily transmitted, and upon them is erected a further psychological structure determined by the experience of each individual by which the accuracy of spatial judgments is considerably increased and their value to the animal augmented.

It will be seen that the two fundamental coordinates are vertical and horizontal in direction, the first determined gravitationally from the earth's centre, the second visually from the horizon. We have already seen that the visual responses of the octopus suggest that these directions have a special status not only in the end-organ but also in its projections onto the primitive central nervous system,¹ a circumstance which indicates their phylogenetic age and practical importance.

Before discussing the part played by spatial perceptions in the behaviour of Vertebrates, it will be useful to discuss the basic physiological factors which underlie such judgments—the mutual relation of the visual fields, the occurrence of binocular as opposed to panoramic vision, and finally the nature of reflex and voluntary ocular movements and their relation to visual perceptions.

THE UNIOCLAR VISUAL FIELDS OF VERTEBRATES

The unioocular field of Vertebrates is relatively constant, averaging in angular size about 170° . The estimation can be made theoretically by optical calculation (Grossmann and Mayerhausen, 1877) or objectively and more effectively by observing the image of a moving light as seen by transillumination through the sclera, a method introduced by the great physiologist, Johannes Müller (1826), in his study of corresponding retinal points, and applied to the determination of the unioocular and binocular fields by Armin Tschermak (1902), Rochon-Duvigneaud (1921–23), Verrier (1930), and others. Following Müller's lead, functional confirmation of these results may be obtained in animals which will respond suitably by the subjective method of noting the angle at which an object will attract attention.

The extent of the field varies essentially with three factors—the angular extent of the retina, the curvature of the optical surface admitting the light, and the effective pupillary aperture. The first of these is the most important, and is relatively constant. Variations,

¹ p. 576.

FIGS. 798 TO 803.—THE UNIOCCULAR FIELDS OF VERTEBRATES.

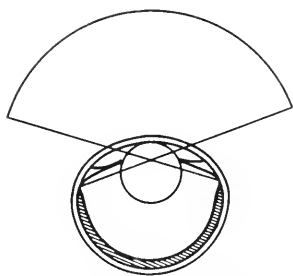


FIG. 798.—A teleostean fish.

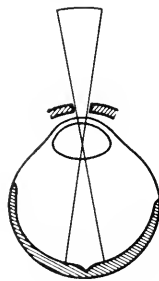


FIG. 799.—The chameleon.

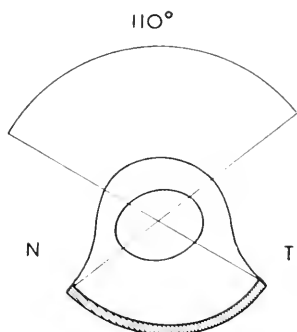


FIG. 800.—An owl.

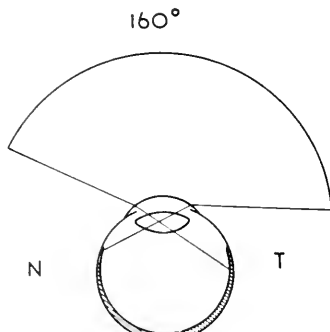


FIG. 801.—A primate.

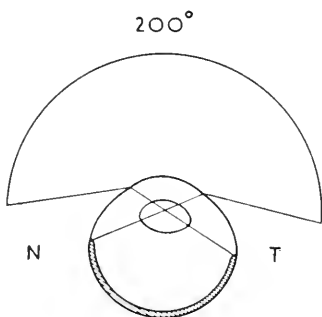


FIG. 802.—The cat.

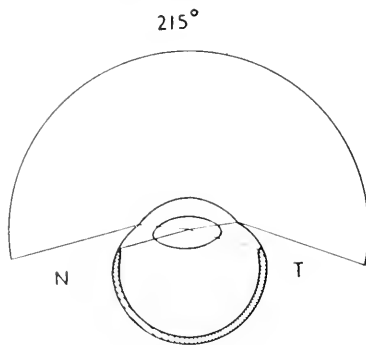


FIG. 803.—The horse.

Horizontal meridian. N, nasal ; T, temporal.

however, occur ; thus the wide visual field of the horse in the obliquely horizontal meridian (215° to 228°) is largely due to the marked forward prolongation of the retina on the nasal side, while the relatively small field of many birds (the owl, 110°) and also of some deep-sea fish is a consequence of the small extension of the retina in their tubular eyes (Figs. 798 to 803).

The curvature of the primary optical surface is also of importance since it determines the extent of the solid angle within which light can be refracted into the eye. Thus the human cornea subtends only 60° of a circle and the visual field averages 150° ; the cornea of the cat forms a much more prominent curve subtending 170° of arc and its visual field averages 200° ; the cornea of the chameleon is largely covered by the lids which leave only a small central aperture roughly

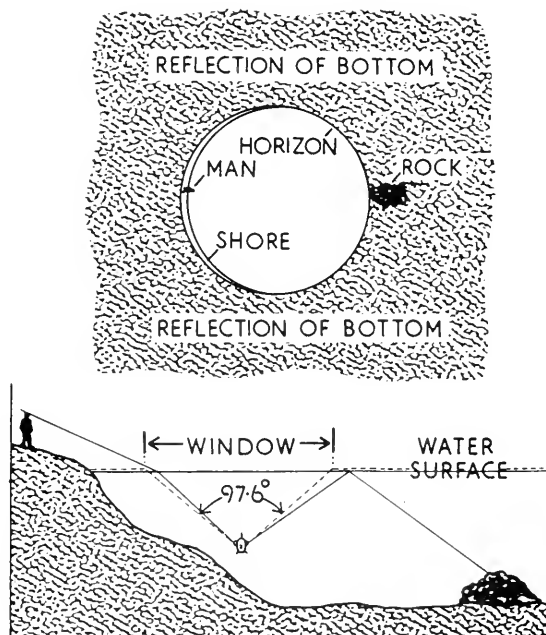


FIG. S04.—THE UPPER VISUAL FIELD OF A SUBMERGED FISH.

In the lower figure the fish is seen swimming in fresh water and the paths of the rays of light are delineated.

In the upper figure is shown the view seen by the fish with the central circular window of aerial vision near the periphery of which bodies become progressively foreshortened; around it is reflected a view of the bottom mirrored on the surface of the water (after Walls).

concentric with the pupil so that it is restricted to tubular vision, a disability neutralized by the extraordinary mobility of its eyes (Figs. 799 and 845). In under-water vision the cornea is ineffective as a refractive element and the lens serves as the determinant of the visual angle; for this reason the lens is circular and situated far forward, closely approaching the cornea in fishes, often protruding beyond the level of the surface of the head; in such an eye the field is determined solely by the angular extent of the retina. The pupillary aperture is a less important factor, but the transversely elongated pupils of

Ungulates such as the horse increase the extent of their field in the horizontal meridian, as does the pear-like elongation of the pupillary aperture in the aphakic area in some teleostean fishes¹ or the key-hole pupil of some arboreal snakes.²

The following estimations have been made of the unioocular visual fields (Figs. 798-803) :

Teleostean fishes—110°-170° (Verrier, 1930).

Lizards—slightly less than 180° (Kahmann, 1932).

Birds—pigeon, 165° ; owl, 110° (Rochon-Duvigneaud, 1921-23).

Mammals—guinea-pig, 135° ; cat, over 200° ; cattle, 205° ; horse, average 190°-195° with a transverse extension to 215° or more (Rochon-Duvigneaud, 1943 ; Bressou, 1955).

The upper visual field of under-water fishes deserves special mention (Fig. 804). When looking directly upwards the fish sees through a "window" into the air ; but in a slantingly upwards direction a progressively greater degree of refraction occurs at the water-air interface until the critical angle is reached (48·8° in fresh water) when the rays of light run horizontally along the surface ; objects in this hemispherical aerial field therefore become progressively smaller, dimmer and foreshortened as the periphery of the " window " is reached. Once the critical angle has been exceeded rays suffer total reflection so that outside his circular " window " the fish must see the bottom mirrored on the surface of the water.

THE BINOCULAR VISUAL FIELDS OF VERTEBRATES

Since the angle subtended by the unioocular field is relatively constant, the extent of the binocular field is determined almost entirely by the position of the eyes in the head. It is often stated that there is a tendency for the eyes to swing from the lateral to the frontal position during the course of evolution so that binocular vision as it is seen in the Primates eventually becomes possible. This, of course, is not the case, for the swing forward in the visual axes has occurred independently many times within the vertebrate phylum, depending on the habits and requirements of different species. Thus most freely swimming fishes have laterally placed eyes but the flat-fishes which lie on the sea-bottom have upward-looking eyes, and in some deep-sea fishes they are directed frontally (Figs. 376, 379) ; the same variation is seen in the Birds which show similar gradations between laterality and frontality, and again in the Mammals. The extent of unioocularity is determined rather by the need of a wide panoramic field for the hunted animal whether it be fish, bird or mammal, for its existence depends on the early detection of enemies in whatever direction, and rapid escape from them (Figs. 805 and 806) ; the extent of binocularity, on

¹ p. 304.

² p. 674.

the other hand, is determined by the greater value of the fine judgment rendered possible by binocular vision in pursuit and attack by the predator, in its ordinary activities by the arboreal animal, or by the Primate the eyes of which have become accurately correlated with the use of its hands. In each species a compromise is reached between the biological value of the reflexes of self-preservation and those of aggression; the former depend on the largest possible total field of vision, the latter on the visual refinements resulting from the near-coincidence of the optic and visual axes when the latter intersect on the fixation point. To attain this end a swing forwards of the optic axes of the primitive

FIGS. 805 AND 806.—BINOCULAR FIELDS.

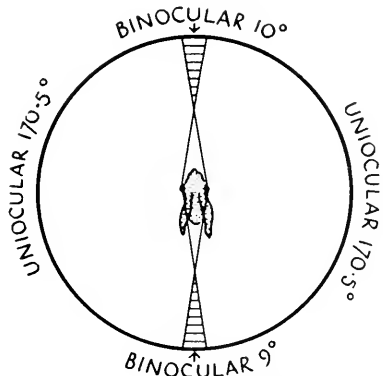


FIG. 805.—The panoramic field of a hunted animal (the rabbit) with a small binocular segment in front (10°) and behind (9°), and a large unioocular area (170.5° on each side).

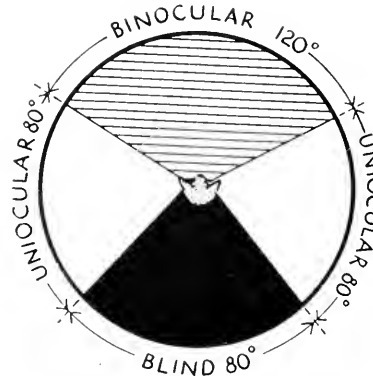


FIG. 806.—The binocular field of a predator (the cat) showing a large anterior binocular area (120°), a large posterior blind area (80°) with relatively small unioocular area (80°).

fish is necessary and since this entails the sacrifice of much of the total field it can only be adopted by animals amply sure of themselves either because of their strength and ferocity or their superior intelligence. The wide panoramic field was undoubtedly the more primitive in evolutionary sequence; frontality for the increased efficiency of binocular vision is attained first by a swivelling forwards of the eyes so that by a reduction of the angle gamma the visual axes, intersecting on the fixation point in front, will more nearly coincide with the optic axes, and secondly, to make this mechanically possible, by a reduction in the divergence of the orbital axes (see Figs. 811-3, 837).

In addition to the biological value of binocular vision as an asset to predacity and fine manipulation, an increase in sensitivity to light may be a third factor in determining its acquirement (Weale, 1955). The binocular sensitivity to light is greater than the unioocular (by 10% in man, Pirenne, 1943). This may account for the parallelism of the visual axes in some strongly nocturnal types such as

deep-sea fishes with tubular eyes or in such species as the owl or *Tarsius*. To such animals a significant lowering of the light-threshold may be of considerable survival-value, while the loss of the panoramic field is compensated by the security of darkness.

Apart from the positioning of the eyes in the head, several devices have been adopted to increase the extent of the binocular field. Most of these we have already noted. Some of them concern the configuration of the eye—the prominence of the corneal curvature (or the



FIG. 807.

FIG. 807.—THE EMERALD TREE-SNAKE, *PASSERITA*.

Showing the deep facial grooves to allow accurate binocular vision (the long body of the animal is coiled up behind the head) (photograph by Michael Soley).



FIG. 808.

FIG. 808.—THE KEY-HOLE SHAPED PUPIL OF THE TREE-SNAKE, *DRYOPHIS*.

To show the aphakic area, the aperture being designed to direct light onto the temporal fovea in the interests of binocular vision.

lenticular curvature in Fishes); the occurrence of a horizontally oval pupil as in Ungulates or some snakes and fishes so that the overlap of the two fields is increased in the horizontal plane; the nasal shift of the lens by the transversalis muscle in turtles, lizards and some snakes (*Dryophis*) on accommodation so that the visual axes are directed forwards more nearly parallel to the axis of the body when the eyes are converging on near objects in front (Fig. 808); and the marked nasal asymmetry of the eye in so many types (many Fishes and lizards, all Birds, Ungulates and Carnivores) whereby the ciliary region is narrowed and the visual retina is allowed to advance far forwards on the temporal side while the cornea and lens are tilted nasally so that the visual axes are encouraged to intersect towards the mid-line. This

tendency may be said to be carried to its extreme in the tubular eyes of some abyssal fishes provided with a lateral accessory retina to overcome the marked deficiency in the field which would result from the use of the main retina alone.¹ In addition, the anatomical configuration of the orbits and skull is frequently modified to eliminate as far as possible any obstruction to the vital frontal field, the most dramatic instance of which is the deep groove running nasally in the cheek of certain tree-snakes in which the eye is set so that it has an



FIG. 809.—THE GOLIATH HERON, *ARDEA GOLIATH*.

To show the deep groove in the skull and bill to allow the accurate fixation of prey by the frontally directed eyes.

uninterrupted view straight ahead (Fig. 807) or the groove in the side of the bill of the heron so that it can see accurately to fixate its prey (Fig. 809).

The first to investigate the extent of the binocular field in the various classes of Vertebrates was Johannes Müller (1826) who measured the angles between the planes of the orbital margins in 190 vertebrate types, making the unjustified assumption that the visual axis was perpendicular to this. These measurements were repeated by Leuckart (1875) and Grossmann and Mayerhausen (1877) and their absurdity soon became obvious. Thus although there is little difference between the optic and orbital axes in most Fishes, there is more in the horse, more still in the cat, while in man the optic axes are almost parallel and the orbital axes diverge by 45° (Fig. 810). A similarly painstaking and elaborate investigation was therefore carried out by the last authors who measured the apparent divergence of the eyes as indicated by the optic axis

¹ p. 323, Fig. 380.

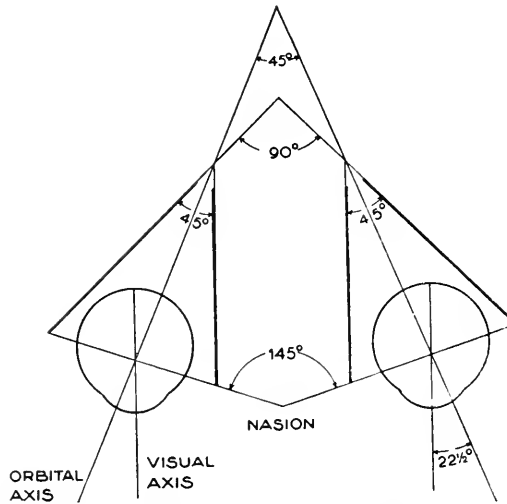


FIG. 810.—DIAGRAM TO SHOW THE RELATION BETWEEN THE ORBITAL AXIS AND VISUAL AXIS IN MAN.

estimated from the centre of the cornea. Unfortunately, however, this method is also gravely at fault since the optic axis rarely coincides with the visual axis—when the latter exists. Indeed, unless there is an area centralis of acute vision through which an animal habitually orientates itself towards an object and around which spatial orientation is centred, the whole concept of fixation along a visual axis is meaningless; only in those animals provided with an area of acute vision is such a concept possible and in these the angle gamma between the optic and fixation axes varies between 5° in man to 80° or 85° in some Fishes or the rabbit with laterally placed eyes (Figs. 811 to 813). When, however,

FIGS. 811 AND 812.—THE ANGLE GAMMA IN VERTEBRATES.

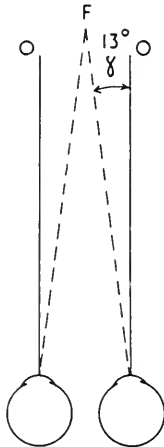


FIG. 811.—The small angle gamma of the cat.

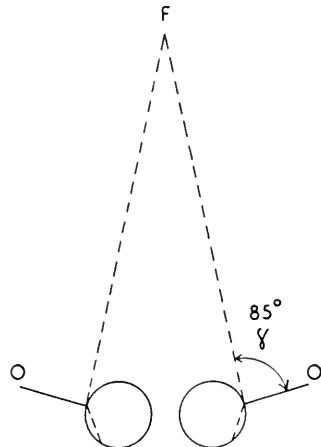


FIG. 812.—The large angle gamma of the rabbit.

The angle γ measures the deviation between the optic axis (O) and the fixation axis (F).

visual axes exist and are nearly central in location, such measurements are of more value ; for this reason Lindsay Johnson's (1901) extensive observations on Mammals give a good indication of the binocularity within this class.¹

The most efficient and reliable method yet evolved for the determination

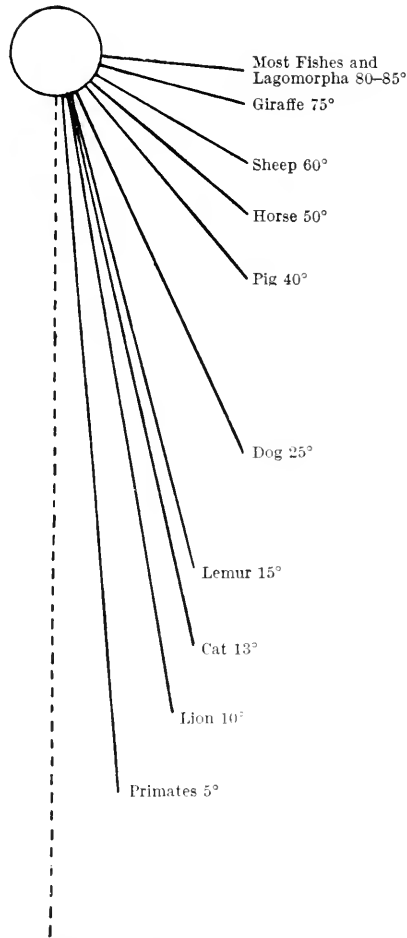


FIG. 813.—THE ANGLE GAMMA IN THE VERTEBRATE PHYLUM.

of the binocular field is that which depends on clamping the dissected head of the animal in the central position on a perimeter, moving a light along the arc and observing its image as seen through the sclera; on moving the light in all directions the extent of the field within which the image falls on the retinae of both eyes simultaneously can be plotted out (Fig. 814). In the hands of Tschermak (1902), Rochon-Duvigneaud (1921-23), Verrier (1930), Kahmann (1932) and Pisa (1939) this technique has given satisfactory results.

¹ p. 688, Fig. 837.

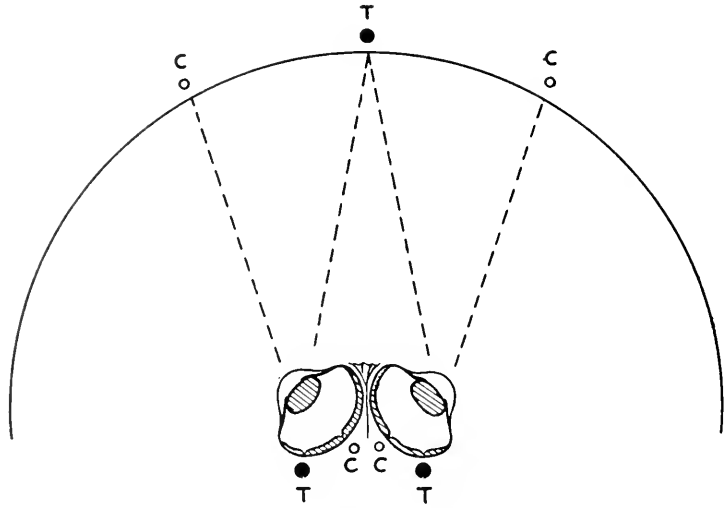


FIG. 814.—THE EXPERIMENTAL MEASUREMENT OF THE VISUAL FIELD.

A light is moved along the arc of a perimeter and the image is seen trans-sclerally behind the globe. The dissected head of the animal (a bird) is clamped centrally. T, temporal, C, central fovea (Rochon-Duvigneaud).



Lamprey

The binocular field of CYCLOSTOMES is small, but with an angle of 160° between its optic axes the lamprey should have an effective although minute binocular field some distance in front of its head.

The binocular field of FISHES is generally relatively small and is represented both in the horizontal and vertical planes. In the usual type of fish with laterally directed eyes and a cigar-shaped body the binocular field is confined to a relatively narrow belt widest in front,

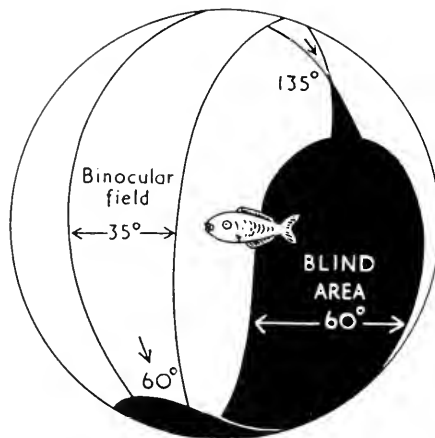


FIG. 815.—THE BINOCULAR VISUAL FIELD OF A TORPEDO-SHAPED FISH WITH Laterally Directed Eyes.

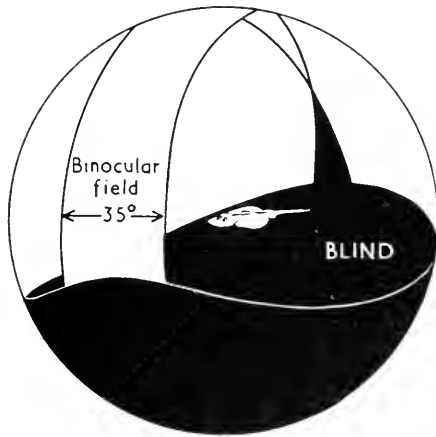
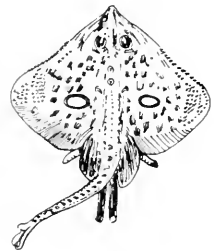


FIG. 816.—THE BINOCULAR VISUAL FIELD OF A FLAT-FISH WITH UPWARDLY DIRECTED EYES.

and extending a considerable distance dorsally (some 135° from the horizontal) and considerably less ventrally (some 60°) (Fig. 815); the area behind and below is often blind. The binocular field in front varies in width considerably, from exceptionally small values of 10° or less (*Box*) to 35° or greater in such active predators as the trout or pike (Verrier, 1930; Kahmann, 1932). The smallest binocular field yet measured in any Vertebrate is that of the gurnard (*Trigla*) of 2° (Verrier, 1928); that of the carp (*Cyprinus*) is very little more (Rochon-Duvigneaud, 1922). Depending on the configuration of the body of the fish a small overlap in the unilateral fields may occur posteriorly, particularly in eel-shaped forms, but it is probably of little functional value (Fig. 817). In bottom-living fishes such as the selachian skates and rays and the teleostean flat-fishes, the binocular fields are increased overhead but not so much as might be expected since the two eyes on the upper side of the head preserve to a considerable extent their lateral



Trout



Ray

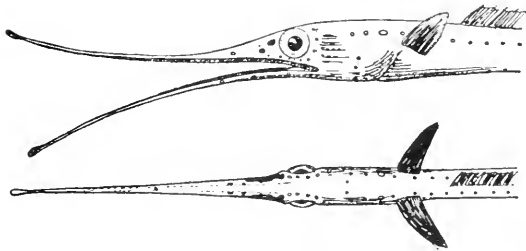
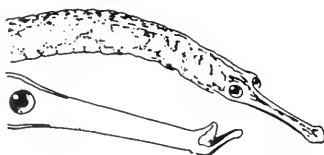


FIG. 817.—THE DEEP-SEA SNIPE-EEL, *BORODINULA INFANS*.

Lateral (above) and dorsal (below) views. Owing to the narrowness of its body and the protrusion of the eyes there is a small posterior binocular field (after Bertin).

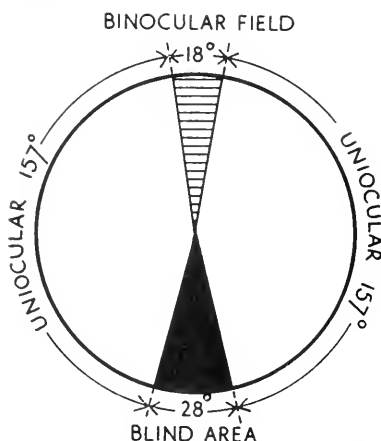
*Opisthoproctus*

direction; they thus retain an extensive panoramic field at the expense of a much larger blind area below, where, resting on or skimming near the bottom, vision is in any event useless (Fig. 816). In other upward-looking fishes such as the stargazer (*Astroscopus*, *Uranoscopus*, etc.) and some abyssal types such as *Opisthoproctus*, the dorsal binocular field may vary between 25° and 40° or even more (Fig. 901). A few pelagic and surface fishes have their eyes canted downwards to produce a small ventral binocular field within which much of their predatory interests lie (the needle-fish, *Belone*; the flying-fish, *Pantodon*).

FIG. 818.—THE PIPE-FISH, *SYNGNATHUS*.

Showing the frontally directed eyes to allow accurate binocular vision in the region of the upturned jaws (seen in profile in the lower figure).

Few fishes have forward-looking eyes; such a configuration occurs in some deep-sea Teleosts provided with tubular eyes (*Giganturus*, etc.),¹ but this overlap of two small fields is probably a device to improve sensitivity in the darkness of the abyss (Weale, 1955). A frontal direction of the eyes with well-developed binocularity may, however, be adopted for reasons of space-perception in the pipe-fish, *Syngnathus* (Fig. 818). As this fish lies immobile on the bottom it catches its prey by opening its jaws just as its victim floats above its mouth; the forward-looking eyes with their temporal foveæ should allow accurate binocular vision in the region of the upturned jaws which protrude far forwards at the end of the elongated snout.

FIG. 819.—THE BINOCULAR FIELD OF THE LIZARD, *LACERTA*.

¹ p. 322, Fig. 379.

FIGS. 820 TO 822.—LATERALITY AND FRONTALITY IN BIRDS.



FIG. 820.—The Barbary turtle dove, *Streptopelia roseogrisea*.
A bird with laterally directed eyes and panoramic fields (Zool. Soc., London).



FIG. 821.—The Chilean eagle, *Geranoaëtus*
(photograph by Michael Soley).



FIG. 822.—Savigny's eagle-owl, *Bubo ascalaphus* (Zool. Soc., London).

Birds of prey with frontally directed eyes and highly developed binocularity and stereoscopy.

The binocular fields of AMPHIBIANS have not been thoroughly explored, but particularly in Anurans it must be of considerable extent (Schneider, 1957).



Trachysaurus

The binocular fields of REPTILES have been extensively studied by Kahmann (1932) who found that they were more constant than in Fishes: the average extent is between 20° and 30° with extremes at 14° in the lizard, *Trachysaurus*, and at 46° in the exceptional tree-snake, *Dryophis*.

Among the Chelonians, as elsewhere in the vertebrate phylum, the extent of the binocular field varies with the habits of the animal;

FIGS. 823 AND 824.—THE BINOCULAR FIELDS OF BIRDS.

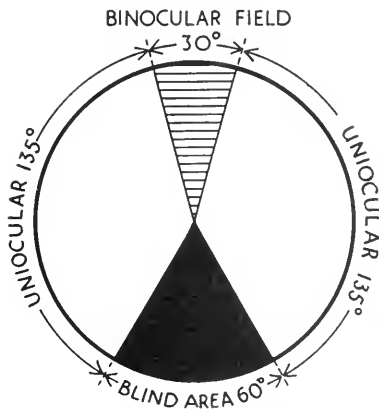


FIG. 823.—The pigeon. Showing a small anterior binocular field, large (panoramic) unioocular areas and a small blind area behind.

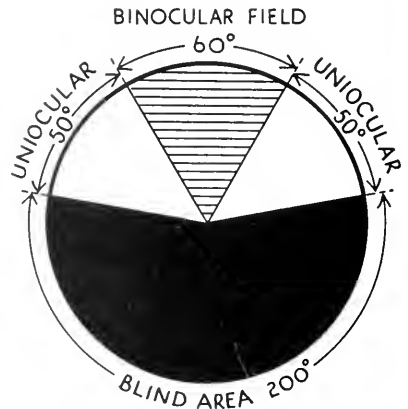


FIG. 824.—The owl. Showing the large binocular field, small unioocular areas, and a large blind area behind, characteristic of a predator.



Clemmys

the smallest is seen in the placid herbivorous tortoise, *Testudo* (18°), the more active terrapin, *Clemmys*, has a field of 34° , while the snapping marine turtle, *Chelydra*, which is an active predator of small fishes, has a binocular field of 38° (Kahmann, 1933).

Those Crocodilians which have been investigated have been found to have a binocular field averaging 25° (alligator, 24° ; cayman, 26°).

Lizards show much the same range as turtles. The smaller types retain a wide panoramic field for protective purposes so that the available binocular range is low—*Trachysaurus*, 14° ; *Anguis fragilis*, 16° ; *Lacerta* and *Iguana*, 18° (Fig. 819); while the larger and more militant types, safe in their strength, enhance their aggressiveness by improved binocularity (*Zonurus giganteus*, 22° ; *Varanus*, 32°).



Iguana

Snakes show a considerable variation in their binocular fields from 20° to 46° . Among representatives of the great central family of

FIGS. 825 TO 827.—THE FOVEAL ARRANGEMENTS OF BIRDS (Casey Wood).

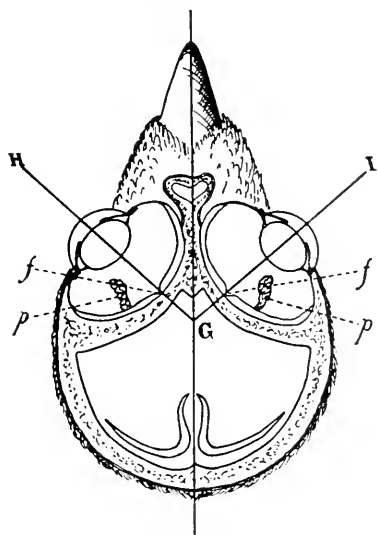
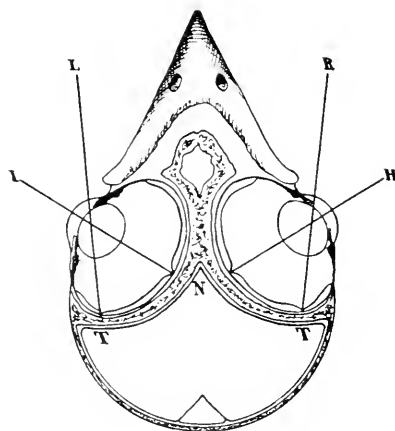
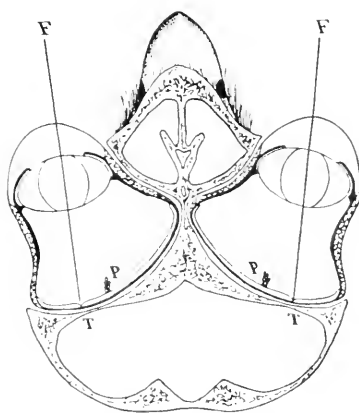
FIG. 825.—The titmouse. To show the laterally directed eyes with central foveæ (*f*) for panoramic vision (visual axes, GH, GI; *p*, pecten)

FIG. 826.—The swallow. To show the laterally directed eyes with central foveæ for panoramic vision (visual axes, LI, NH) and temporal foveæ for binocular vision (visual axes, TI, TR).

FIG. 827.—The owl. To show the frontally directed eyes with temporal foveæ for binocular vision (visual axes, TF; *P*, pecten).

Colubrids the binocular field is very variable (*Coluber*, 20° ; *Tarbophis*, 24° ; *Zamenis*, $28-32^{\circ}$; *Tropidonotus*, $34-42^{\circ}$; *Malpolon*, 38° ; *Uromacer*, 40° ; *Dispholidus*, 42°), as also in the more primitive Boidæ (*Constrictor*, 34°), while, as we have noted, the active tree-snakes (*Dryophis*, *Passerita*) have the maximal binocular field of 46° .

The binocular fields of BIRDS may be classified into two distinct types—that of birds with narrow heads and laterally directed eyes with a central fovea, which have a wide panoramic field of about 300° and a relatively small binocular field varying from 10° or less (6° in

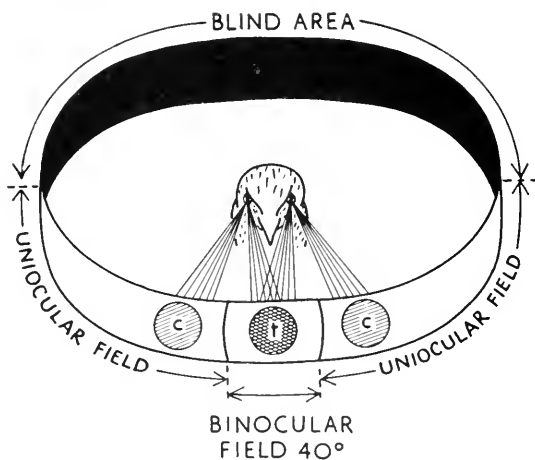


FIG. 828.—THE VISUAL TRIDENT OF BIRDS OF PREY.

The foveal projections in the hawk. *c* and *c*, the projections of the central foveæ for panoramic searching. *t*, the projections of the two temporal foveæ for stereoscopic vision in attack (after Rochon-Duvigneaud).

parrots) to 30° (Figs. 820 and 823), and that of birds with rounded heads and frontally directed eyes which have a relatively small total field of about 180° with a relatively large binocular segment varying from 35° or 40° to 60° or 70° (Figs. 821-2 and 824). As occurs in most species of animal the former are timorous in type and granivorous in habit; their survival depends on early awareness of an enemy and rapid flight; typical examples are the song-birds or the pigeon. Those with an extensive binocularity are the predators—the swallows, the falcons, the hawks, the eagles, the owls, and so on—and in these, while the laterally-looking central foveæ are ideal for searching, the temporal foveæ have a common projection straight ahead in the binocular field so that their judgment of distances for swooping on their prey while in rapid flight attains an accuracy which can only be described as extraordinary (the VISUAL TRIDENT of Rochon-Duvigneaud, 1933) (Figs. 825 to 828).



Eagle

While these constitute the main types of field in Birds, it is to be expected that in a class so diversified exceptions exist. Some penguins (*Spheniscus*) have no binocular field. The snipe has eyes set far back in its head giving a considerable posterior binocular field so that it can see a potential enemy behind and



FIG. 829.—THE BITTERN, *BOTAURUS STELLARIS*.

A delightful photograph showing how adept the bittern is at concealment. When disturbed among the reeds it stretches its neck with the beak pointing upwards and stands motionless so that the dark stripes running down the neck and breast feathers blend with the reeds among which it hides. In the meantime, the downwardly directed eyes get an unimpeded view and the bird is enabled at the same time to watch its brood at its feet (Burton's *Story of Animal Life*, Elsevier Pub. Co.).

above when feeding, while the bittern with its downward-pointing eyes has a ventral binocular field so that it can still see downwards with both eyes when standing camouflaged among the reeds with its beak pointed upwards towards the sky to simulate another reed (Fig. 829). Occasionally a single type may differ widely from the characteristics of the family ; thus alone among parrots the kakapo of New Zealand (*Stringops labroptilus*) and alone among ducks the



Stringops

THE EYE IN EVOLUTION

FIGS. 830 TO 834.—PANORAMIC VISION IN PLACENTALS.

FIG. 830.—Prejvalski's horse,
Equus przewalskii.FIG. 831.—Somali wild
ass, *Equus soma-*
liensis.FIG. 832.—Cotton's giraffe,
Giraffa camelopardalis.

To show the configuration of the eyes for panoramic vision in Ungulates. The laterally directed eyes of the horse have a considerable binocular field particularly in the horizontal direction (see Fig. 838). In the giraffe, because of its long neck, the eyes are directed downwards to obtain the greatest field on the ground (Zool. Soc., London).



FIG. 833.



FIG. 834.

FIGS. 833 AND 834.—The positioning of the eyes in the rabbit to allow for the wide panoramic field (see Fig. 805).

blue duck of New Zealand (*Hymenolæmus malacorhynellus*) have frontally-directed eyes and considerable binocular fields.

The binocular fields of MAMMALS also vary within wide limits (Figs. 830-9). Some, particularly timid types, have divergent optic axes and a small binocular field ; in others, particularly predators, the optic axes tend towards frontal parallelism and the binocular field is more extensive. The first class is exemplified by the Rodents. In the rabbit there is an overlap of the circumferential unocular fields

FIGS. 835 AND 836.—BINOCULAR VISION IN PLACENTALS.

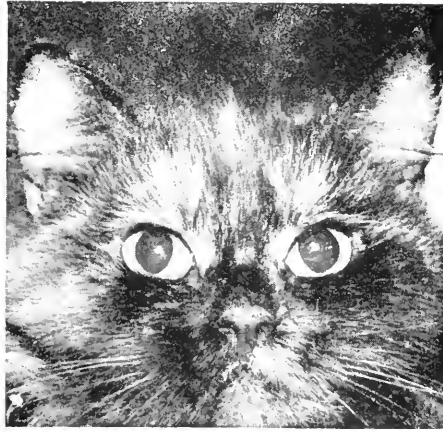


FIG. 835.—The cat.

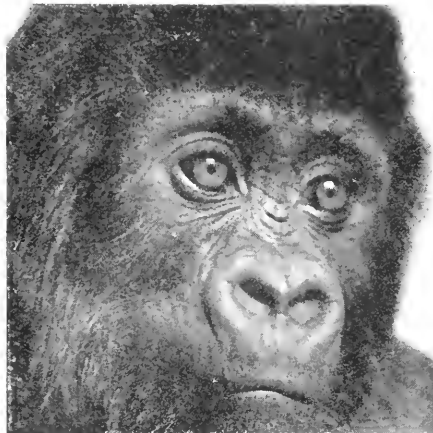


FIG. 836.—The gorilla (Zool. Soc., London).

In the cat frontality is required for predatory purposes (Fig. 806) ; in the primate for finesse in manipulation (Fig. 839).

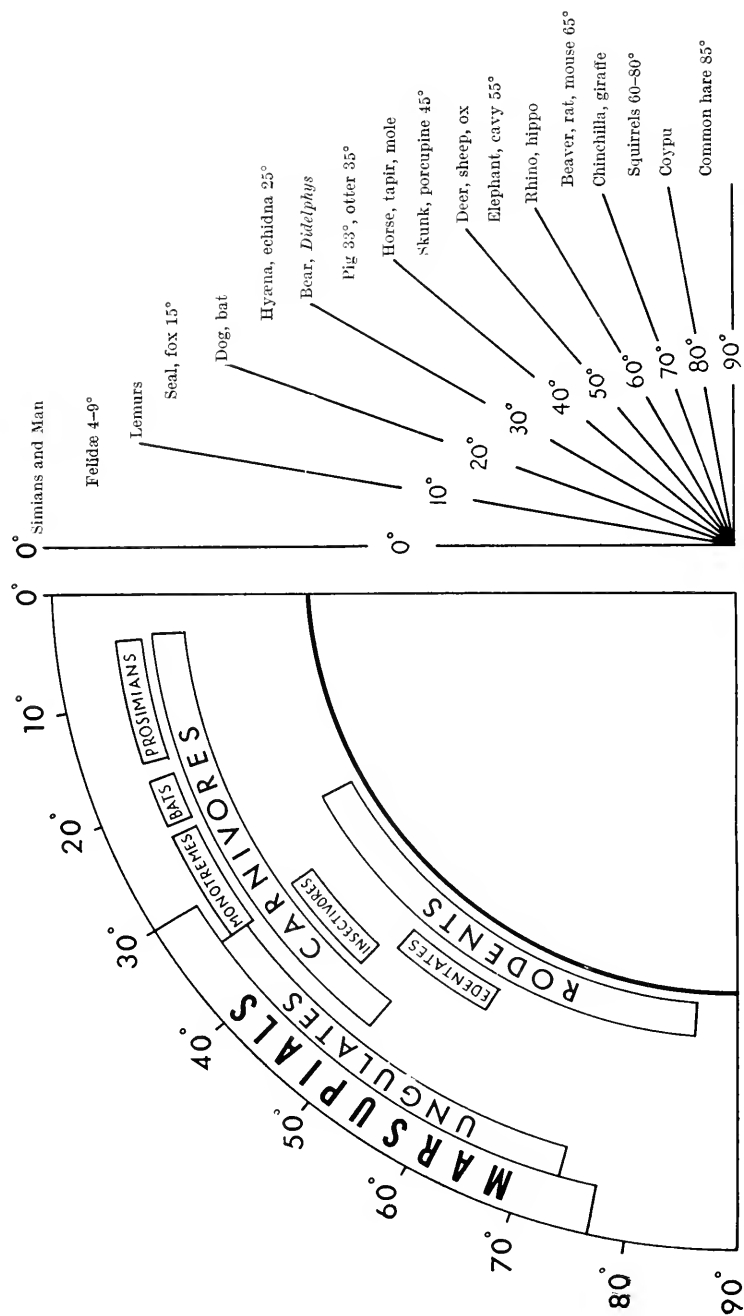


FIG. 837.—THE ANGLES BETWEEN THE OPTIC AXES AND THE MID-LINE (THE BODY AXIS) IN MAMMALS.
Families and species on the right; orders on the left (Lindsay Johnson).

so that binocularity is attained both in front (10°) and behind (9°) (Dubar, 1924 ; Pisa, 1939) (Figs. 805, 833-4). In the squirrel with its protruding eyes the binocular field is more extensive and varies from $25-30^\circ$. The Ungulates occupy an intermediate position with a binocular field varying from 60° to 80° (Kahmann, 1933). The horse has a wide binocular field in front ($60^\circ-70^\circ$) and a wide panoramic unioocular segment of 146° so that it sees behind along a line parallel to the axis of its body (Figs. 830-1, 838) ; by adopting a number of devices such as the forward prolongation of the functional retina on the nasal side, and the horizontally oval pupil, this animal thus



Squirrel

FIGS. 838 AND 839.—THE BINOCULAR FIELDS OF PLACENTALS.

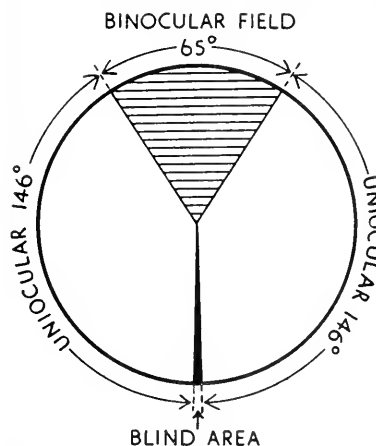


FIG. 838.—The horse. Showing a small binocular field, large panoramic unioocular areas and a minute blind area.

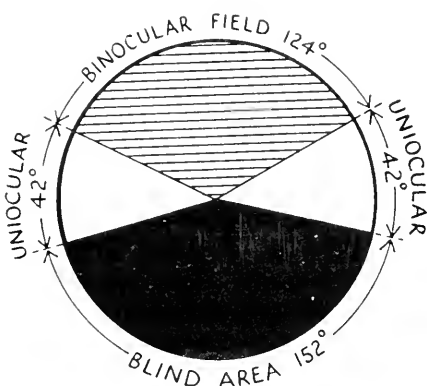


FIG. 839.—A primate. Showing a large binocular field, small unioocular areas and a large blind area.

achieves a remarkable field, with a broad binocular area in front and below to survey the ground on which it is feeding or over which it is galloping, and a minimal blind area behind. The elephant has the wide unioocular area of 190° and a binocular field of 67° . The goat has a binocular field of 63° , the ox of $51-78^\circ$ (Pisa, 1939 ; Bressou, 1955). Carnivores with eyes set more frontally have larger binocular fields, that of dogs varying from 80° to 116° (Thieulin, 1927) and of cats extending to 120° (Fig. 806) ; while in monkeys, apes and man it may extend to 140° —in this class, as we have seen, in the interests of finesse in manipulation (Fig. 839).

THE OCULAR MOVEMENTS OF VERTEBRATES

Ocular movements in Vertebrates are of three types all of which are of primary importance in spatial perceptions :

(1) Involuntary movements, associated with the postural reflexes



Spider monkey

the essential purpose of which is compensatory in nature, tending to maintain the visual field as far as possible in its normal orientation.

(2) Voluntary movements made spontaneously for the purpose of changing the visual field to allow the deliberate exploration of space. While the involuntary movements tend to maintain constancy in the visual field, voluntary movements are designed to achieve its variation.

(3) Reflex corrective movements associated with fixation and fusion.

It is interesting that apart from retraction and elevation (movements associated with the contact reflex of the cornea and with swallowing¹), no ocular movements have been seen in Anurans ; nor have they in Crocodilians but these reptiles have received little study in this respect ; while in many Birds the eyes are immobile and even reflex involuntary movements are often largely undertaken by the unusually flexible neck.²

INVOLUNTARY OCULAR MOVEMENTS. We have already seen that the primary function of vision is to control the movements of the animal ; indeed, the primitive photokineses and phototaxes of the lower Invertebrates survive in the fundamental postural reflexes of the Vertebrates. The early aquatic Vertebrates (Cyclostomes, Fishes, Urodeles and larval anuran Amphibians) were provided with an elaborate system of lateral line organs attuned to respond to vibrations in a watery medium associated with a labyrinth designed to subserve a postural mechanism. When Vertebrates left the water for land the lateral organs disappeared to be replaced by a new organ, the cochlea, designed to respond to vibrations in the new medium (air), but the labyrinth was still retained and was associated with proprioceptive impulses from the neck and limbs. The stimuli from the lateral organs and the labyrinths were carried to the tegmentum and the tectum where they were associated with visual stimuli ; the stimuli from the more lately developed organs took a similar course, and in the mid-brain an important group of centres became aggregated controlling the reflexes concerned with the acquirement and maintenance of posture and associating them with the eyes.³ The mechanism involved is elaborate and has been elucidated in a classical series of researches by the great Dutch physiologist, Rudolf Magnus, and his associate, de Kleijn, whose work was inspired by Sherrington's analysis of the phenomena of decerebrate rigidity.⁴ To the basic concepts advanced by these workers little fundamental has yet been added.

The primary function of the ocular movements was therefore

¹ p. 345.

² p. 695.

³ See Figs. 712-5.

⁴ See Sherrington, 1904-6 ; Magnus, 1924.

postural in nature, designed to maintain the visual field constant in spite of the movements of the animal; the primary function of the extra-ocular muscles, to put the matter paradoxically, was to keep the eyes immobile *in space*. In Cyclostomes and most Fishes this is the only type of movement which exists, and every movement of the head is

FIGS. 840 TO 842.—POSTURAL REFLEXES.

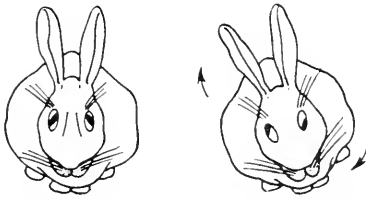


FIG. 840.—Tonic labyrinthine reflexes.

The rabbit on the left is in the normal position; the rabbit on the right has been rotated so that its right side becomes lower, and the movements of the eyes are indicated by the arrows (after Magnus).

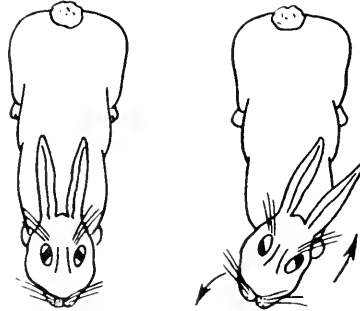


FIG. 841.—Tonic neck reflexes.

On rotation of the head upon the trunk the movements of the eyes are indicated by arrows.

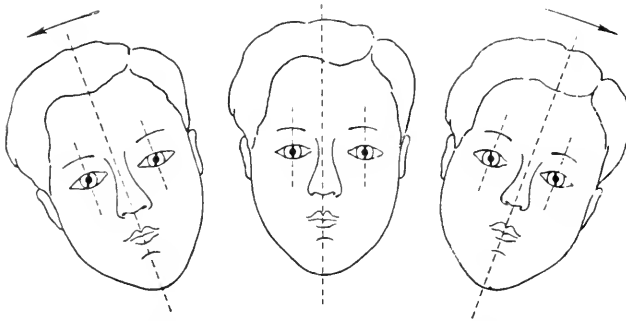


FIG. 842.—Compensatory movements of the eyes on inclination of the head.

associated with a compensatory movement of the eyes. For this reason the extra-ocular muscles of Fishes have a uniquely simple arrangement designed merely to accomplish horizontal, vertical or wheel rotatory movements, the recti taking origin from the apex of the orbit and rotating the globe around the vertical and transverse axes, the obliques arising from the orbital margin and rotating the globe around the antero-posterior axis (Fig. 293). Such movements

are found throughout the entire vertebrate phylum in all animals wherein ocular movements occur, so that in postural attitudes the eyes, so far as is possible, maintain the same position in space, while the head revolves around them (Figs. 840 to 842). It is important to remember that the static postural reflexes are not associated with vision and for this reason they occur in the blind and in the decerebrate animal.

These ocular movements are precisely correlated with the bodily movements; their regularity is seen when their excursion is plotted diagrammatically in the form of a graph. Fig. 843 illustrates such a graph taken from Benjamins (1920) on fish: positive values indicate deviations of the anterior pole of the cornea

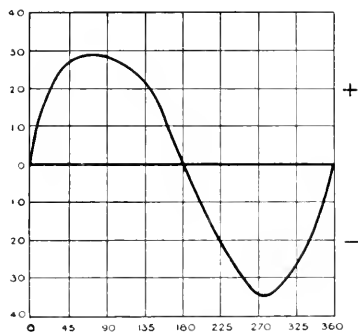


FIG. 843.—ROTATION OF THE EYE OF THE PERCH ABOUT THE VISUAL AXIS IN RESPONSE TO ROTATION OF THE BODY ABOUT A TRANSVERSE AXIS.

Positive values indicate deviations of the anterior pole of the eye towards the belly; negative towards the back.

The ordinates indicate the angle through which the anterior pole of the eye has rotated. The abscisse indicate the position of animal in degrees (Benjamins).

towards the belly, negative values towards the back; the ordinates represent the angle through which the eye has rotated.

The ocular movements take place with extreme rapidity, their latent periods being measured in milliseconds in contrast to the slow postural adjustments of the head and limbs. de Kleijn established that rabbits can compensate head movements of 100° about a bitemporal axis with ocular movements of a rapidity of this order. In the pigeon compensation is perfect only up to movements of 10° and the eyes move back either by a slow drift or a quick flip so that during flight accurate fixation of the next landing point is rapidly possible (Whitteridge, 1956). In man compensation is complete during head movements of up to 30° and it is interesting that during the excursion visual acuity is not affected (Merton, 1956).

VOLUNTARY OCULAR MOVEMENTS. Voluntary movements of the eyes are a later evolutionary development adopted in the interests of vision as a perceptual process. Within the vertebrate phylum an important evolutionary step is seen. *In all Vertebrates below Mammals*

(with the exception of the occurrence of reflex corrective movements for convergence in a few species) *voluntary movements are incoordinated in the sense that the eyes move independently of each other*. In Mammals, and in Mammals alone, the ocular movements are coordinated in the sense that the movements of both eyes are conjugated with a considerable degree of exactitude. In the former case the movements are generally staccato and quick; in the latter they tend to be deliberate. In the former case neither eye moves symmetrically or synchronously with its fellow for not only may the eyes move in different directions at the same time, but one may move while the other remains fixed. In the first case there is a complete decussation of the optic nerve fibres at the chiasma (with the known exception of a few fibres in some snakes)¹ and each retina is projected in its entirety onto different hemispheres of the cerebral cortex; in the latter case there is a partial decussation at the chiasma and both retinae are projected onto each hemisphere of the cortex.

Among FISHES spontaneous ocular movements are relatively rare and as a general rule the visual field is changed or a moving object is followed by movements of the body while the eyes remain still. Spontaneous movements occur, however, in several species of active and lively pelagic fishes particularly those with a fovea,² for in these types fine ocular movements are essential if an area specialized for visual acuity is to be usefully employed for fixation. But in these fishes, apart from temporary convergence of the temporal fovea upon prey in some species, the eyes (and foveae) are used unioocularly, and even those types which have a temporal fovea quite frequently use it for unioocular fixation as well as for convergence (the blenny, *Blennius*; the sea-bass, *Serranus*; the Hawaiian wrasse, *Julis*; the weever, *Trachinus*, etc.); they are, indeed, the only Vertebrates which can employ a temporal fovea unioocularly (Walls, 1942). Exceptionally sluggish fishes such as the sea-horse, *Hippocampus*, and the cling-fish, *Lepadogaster*, show quick, darting and wholly dissociated movements of the eyes resembling those of the chameleon; while bottom-fishes such as the flounders (Pleuronectidae) and the soles (Soleidae), when they lie half-buried in the sand, explore the surrounding water by independent movements of their pediculated eyes. Rochon-Duvigneaud (1943) observed small independent movements of the eyes in types such as the carp, *Cyprinus*, and the European wrasse, *Labrus*, as they lay immobile on the bottom of an aquarium.

A greater degree of movement is sometimes seen in atypical fishes with eyes adapted for aerial vision. Thus in the Indian mullet, *Mugil*, which swims along the surface feeding upon algæ and caddis-fly larvæ,



Serranus



Hippocampus



Sole

¹ p. 392.

² p. 309.

the protruding eyes, well raised above the water to search for a meal, are freely motile, particularly antero-posteriorly; this motility is matched only by the chameleon-like movement seen in the turreted eyes of the mud-skipper, *Periophthalmus*, as it skips about on land upon its fins seeking its insect food in the search for which the eyes move about in all directions, even downwards, as if set upon universal joints (Fig. 844).



Triturus (female)

The eyes of AMPHIBIANS, whether Anurans such as the frog or toad or Urodeles such as *Triturus* or *Salamandra*, have never been observed to exhibit voluntary movements, although the lizard-like insect-catching habits of many would suggest that these would be biologically useful.



FIG. 844.—THE MUD-SKIPPER, *PERIOPHTHALMUS*

The fish is on land and the prominent, freely-motile turreted eyes are well seen (c.f., Fig. 386) (photograph by Michael Soley).

REPTILES with some marked exceptions are not characterized by active ocular motility; most of them when quiescent maintain complete immobility of the eyes. Rochon-Duvigneaud (1943) divided them into two types: the first—crocodiles, geckos and snakes—with a wide palpebral fissure and an extensive field, in which the eyes appear to be immobile; the second—Chelonians and most lizards, particularly the chameleon—with a small palpebral aperture and with mobile eyes. The turtles and tortoises, like some teleostean fishes, can coordinate their eyes in lateral movements for binocular vision, but all vertical movements are independent. The more active lizards show a considerable ocular motility—in *Lacerta viridis*, the excursion is 40° —but all voluntary movements are independent and incoordinated; in the more sluggish and many nocturnal forms the eyes are relatively immobile; in some forms, such as the Gila monster, *Heloderma*, ocular movements are apparently absent; but the chameleon is notorious in the animal kingdom for the extraordinary excursion and rapidity of the movements of its eyes (Rochon-Duvigneaud, 1933).



Heloderma

The eyes of this animal bulge from the head while the small circular palpebral aperture considerably restricts the visual field¹ (Fig.

¹ p. 671.

845) ; in seeking and catching insects a high degree of ocular mobility is therefore essential; moreover, as in the sea-horse, the movements of the body are sluggish and the eyes and the tongue are the only parts of the animal to exhibit the activity necessary to maintain its livelihood. As it sits motionless, the eyes constantly and diligently explore the surrounding environment unioocularly, swivelling like turrets through an angle of 180° horizontally and 90° vertically in complete incoordination, one eye, for example, looking straight forward while the other looks backwards. When an insect is seen, however, the eyes suddenly become coordinated in extreme convergence so that both central foveæ



FIG. 845.—THE CHAMELEON, *CHAMELEON DILEPIS*.

The freely-motile eyes with the minute palpebral apertures look in different directions (c.f., Fig. 420) (photograph by Michael Soley).

are brought to bear upon the prey, and the long sticky tongue, impelled by its own elasticity and by the forcing of blood into the hollow spaces within it, shoots out as far as the length of its body with extreme rapidity and infallible accuracy to catch any insect within its reach.

Snakes show little ocular motility ; swinging the head from side to side pendulum-like, they examine an object first with one eye and then with the other and then binocularly. the head-movements taking the place of ocular movements ; even those possessed of a temporal fovea, such as the tree-snakes,¹ do not require to converge their eyes to achieve binocularity.

BIRDS, because of the enormous size of their eyes filling the bony orbits, have necessarily very restricted movements—if any. Slight horizontal movements are often the only ones to be represented : the eyes of the owl, for example, cannot be moved passively even with a

¹ p. 388.



Cormorant

pair of pliers. To a large extent this immobility is compensated, as in snakes, by the extreme mobility of the neck, the constant agitated swivelling and nodding movements of the head continually varying the visual fields; the hawk, for example, can swivel its head around through an angle of 180° , the owl, of 270° . Moving objects are thus followed by movements of the head and gross ocular reflex movements are taken over by neck movements. The presence of two foveæ also lessens the need for movements of the eyes while the nasal asymmetry of the eye and its dioptric elements supply the amount of convergence necessary for the binocular function of the temporal foveæ so that

FIG. 846.—A DRAWING OF *TARSIVS*.

Looking directly behind itself; to show the extraordinary mobility of the neck to compensate for the immobility of the eyes.

convergent movements for this purpose are not usually required. It is true that limited ocular movements are seen in some species, particularly the parrots, large-beaked birds such as the hornbills or the toucan, and aquatic birds such as the crane, the seagull, the penguins and the cormorant (Rochon-Duvigneaud, 1943). In these, however, movements of the two eyes are always dissociated except for movements in the horizontal field in the interests of convergence.

MAMMALS are unique in their ocular movements, whether lateral, vertical, oblique or convergent, in so far as they are always conjugated. In the lower classes, however—Insectivores, Chiroptera, Edentates and Rodents—movements are very restricted, if, indeed, they exist; even visually conscious

Rodents such as the squirrel and the marmot hardly move their eyes although they are busily engaged in exploring space intently all the while, doubtless because in their cone-rich retina visual acuity is everywhere excellent (Rochon-Duvigneaud, 1943); conversely in the mouse or the rat the eyes are kept motionless, probably because vision is everywhere so poor (Walls, 1942). In Ungulates ocular movements are more conspicuous; the eyes of the elephant, however, are relatively immobile despite the enormous size of the extra-ocular musculature.¹ In the larger Carnivores of the cat and dog families, they are freer; and in the foveate higher Primates they are most conspicuous of all. In all cases, however, as in man, they are largely supplemented by movements of the neck, and the head is

¹ p. 497.

usually turned so that an object of attention is brought within the binocular field ; even in a Primate such as *Tarsius*, the large eyes of which are practically immobile, ocular movements are largely taken over by movements of the neck which can rotate through an angle of 180° so that the animal can look directly behind without inconvenience (Fig. 846).

UNIOCULAR AND BINOCULAR VISION

It has often been implied, and indeed said, that animals with laterally placed eyes and panoramic vision and with a total chiasmal decussation cannot fuse the two uniocular fields ; the logical implication is that two separate uniocular impressions are appreciated so that the only alternative to rivalry or diplopia in the binocular field would be that suppression alternates between the two retinae. Partial decussation of the sensory paths and the projection of each half-field onto the same hemisphere has thus been taken as the anatomical basis of fusion and stereoscopy. Such a view is without firm foundation. It is our universal experience that visual impressions from our semilunar uniocular fields, the afferent fibres from which suffer complete decussation and are relayed to separate hemispheres in the cortex, are inextricably mixed without rivalry with those from the binocular field and form a unity with them ; the sensory impression is comparable to our unitary appreciation of an object such as a pencil when touched with the fingers of each hand. There is no reason why the uniocular fields of animals cannot be fused to form a single perceptual whole even although they are appreciated by different halves of the brain just as, if we close one eye, the two segments of the resulting uniocular field are seen as one although they are perceived by the synthesis of the activity of different cortical hemispheres. The whole behaviour of Vertebrates, the preference for binocular vision when visual accuracy is required, and the extreme accuracy in spatial judgments of bifoveate vision in a chameleon or a bird of prey justify the conclusion that, despite total decussation at the chiasma, the Vertebrates below Mammalia enjoy binocular single vision with a considerable degree of depth perception and stereopsis in the overlapping parts of the fields owing to the appreciation of binocular parallax clues. In all Vertebrates, whether they are provided with a complete or partial decussation of the optic nerve fibres, binocular vision is a perceptual process, the singleness of which represents the product of a synthesis which is built upon already elaborated uniocular sensations.

The historical evolution of these ideas is interesting. The structural hypothesis, depending on the direct continuity of the neural apparatus particularly as seen at the chiasma, was taught by Galen¹ and elaborated by Isaac

¹ *De usu partium corporis humani*.

Newton (1704), Wollaston (1824), J. Müller (1826) and others. An alternative view explained the phenomenon of binocular vision by denying its existence and assuming that one eye only was able to see at a time ; this was originally offered by Porta (1593) and elaborated by Gassendi (1658) and du Tour (1743), and in more recent times by such natural philosophers as Wundt (1862). A third view, originating with Kepler (1611) and elaborated by Porterfield (1759) and maintained by such observers as Sherrington (1906) and Ovio (1927), postulated a purely perceptual basis for the phenomenon ; so far as sensory perception is concerned the chiasmal decussation or the laterality of the cerebral terminal is immaterial, for a mental synthesis can deal with either topographical scheme.

It would appear that a reservation may have to be made in this generalization in the phenomenon of the *interocular transfer of impressions*. In man, an eye trained to a task while the other eye is occluded can automatically be replaced by the latter without detriment to his performance ; in infant chimpanzees such a transference is not complete but the task can be re-learned by the second eye very readily (Chow and Nissen, 1955). In fish, however, Sperry and Clark (1949) found that this did not appear to be the case ; if gobies (*Bathygobius*) were trained to swim towards the upper of two objects with one eye occluded, occlusion of the other eye was followed by a large increase in mistakes which were immediately rectified when the first eye was again occluded. In pigeons, however, Seigel (1953) found that they were able to effect immediate transfer of a circle-versus-triangle discrimination from an eye used in training to the other not so used ; such an immediate transfer occurs in cats even after section of the crossed fibres of the chiasma (Myers, 1955).

If decussation of the optic nerve fibres is without great sensory significance, the occurrence of partial decussation in the Placentals and the gradual increase in the number of uncrossed fibres until they reach almost 50% of the total in the Primates—presumably a progressive element in evolution—must receive some other explanation. The fact remains that (with the exception of the presence of some non-decussating fibres in snakes the significance of which is unknown) in animals below Placentals decussation is complete no matter how large the binocular field, in Placentals decussation is partial no matter how small the binocular field. It is obvious that if a high degree of stereoscopic vision is to be attained, a mechanism of extreme exactitude must be developed to ensure that, so far as it is possible, the two eyes move as a unity, preserving a mutual relationship so that in all positions the images of each object binocularly fixated will fall on corresponding points of the retinae which have become functionally associated with each other. If adequate motorial coordination is to be attained it is essential that the two eyes be controlled by the higher centres as a unitary organ ; just as binocular sensations are regarded introspectively as balanced in the median sagittal plane of the head, the taxis of the eyeballs must be transferred each from its own sagittal plane to the median sagittal plane of the body. As is seen in the limbs, the taxis of the muscles situated (functionally) to the right (for example, the right external rectus and the left internal rectus) is entrusted to

the left hemisphere. Although the projection of the two corresponding retinal areas upon the same cortical field is not essential for the fusion of their several sensory impressions, such a confluence of sensory conductors is necessary, as was pointed out by Mott (1905) and Sherrington (1906), if they are to have access to a common efferent (motor) path which both must use if a coordinated mechanism is to result.

The complete decussation of the optic nerve fibres at the chiasma in Vertebrates below Mammalia and their partial decussation in Mammalia is thus associated with the fact that the latter is the only class of Vertebrates wherein the ocular movements are coordinated. Moreover, the latter is the only class of Vertebrates wherein the ocular motor nuclei in the mid-brain, particularly those of nerves III and VI, are intimately related with a system of crossed association fibres (Kappers, 1920). The anatomical association of the visual fibres is thus an evolutionary adaptation correlated with motor rather than sensory events, and marks a distinct stage in the progress of the development of binocular vision into a highly integrated mechanism of ever-increasing exactitude. Without complete motor coordination the continually shifting system of local signs of direction characteristic of animals with uncoordinated eyes could not have been replaced by a functionally established system of corresponding points and accurately fixed local signs of direction, nor would it have been possible to introduce additional clues to the judgment of distances such as physiological diplopia. With such coordination, community of sensation becomes reinforced by community of action. Significantly, the appearance of such coordination in Mammals coincides with the fact that in these, for the first time, the visual processes are transferred from the tectum and the mid-brain to the cortical level¹; only in Mammals, therefore, is such coordination possible.

Kappers (1920) accounted for the partial decussation of the visual fibres by the theory of NEUROBIOTAXIS, a hypothesis by which he has endeavoured to explain the complicated migration of nerve centres and nerve tracts in phylogenetic history, and the seemingly peculiar location and relation in which this has resulted in the higher animals. In its essentials the theory postulates that the migration and final arrangement of neural elements are determined by an association of function, the determining force being physico-chemical. The intimate nature of such a force or the manner of its action is, of course, highly speculative—and admittedly so; but such a conception, correlating structure and function, is essentially rational in its biological implications, and clears up many difficult points in the anatomy of the central nervous system of the higher animals, in its comparative anatomy, and in its embryology.

Those parts of the central nervous system which are associated with the photostatic functions of vision provide several peculiarly apt illustrations of this theory. The most outstanding, perhaps, is the position of the oculomotor

¹ p. 543.

nuclei, with their close anatomical relationship to the posterior longitudinal bundle and the vestibular system, their secondary changes in position corresponding to changes in the paths of the optic, vestibular and coordinative reflexes. In the present case, when the eyes are directed frontally but are in a non-converging position, the nasal fibres of one retina and the temporal fibres of the other are stimulated simultaneously by laterally incident light; these fibres therefore run in contiguity in the central nervous tract. Again, with frontally incident light, the image is formed on the temporal sides of the retinae of both eyes. Thus the temporal region of one retina works partly with the opposite temporal region and partly with the opposite nasal region, whereas the nasal regions never work together. Hence the temporal fibres from both sides must also run in contiguity, and therefore there are both direct and crossed (macular) temporal fibres in each tract.

Associated with the motorial coordination of the eyes the *pupillary reactions* are interesting. There is a consensual pupillary reaction in the selachian rays and in the pigeon, but so far as is known in all the other lower Vertebrates wherein the pupils react to light—Fishes, Amphibians, Reptiles and Birds—the reaction is unilateral and confined to the stimulated eye (Rochon-Duvigneaud, 1943). In the lower Mammals such as the Rodents the same unilaterality obtains; a faint consensual reaction is seen in Carnivores such as the cat and dog in which the non-decussation of nerve fibres becomes considerable; while only in Primates wherein a hemi-decussation occurs do the sensory and motorial reactions become fully conjugated and the responses of the two pupils become almost equal when one eye is stimulated.

SPATIAL JUDGMENTS

While no systematic research has been devoted to the subject, the visual performance of Vertebrates leaves little doubt that spatial perceptions of some accuracy are a universal attribute of vertebrate vision, probably crude in the uniocular field, often of great accuracy in the binocular field and sometimes of incredible accuracy with bifoveate vision. If we reason from our own subjective impressions—always, it is to be remembered, a most dangerous thing to do—it is probable that in the uniocular field these perceptions are derived from such factors as the retinal size of the images of known objects, overlap of contours, the placement of shadows, aerial perspective and uniocular parallax, often with the help of accommodation. Within the binocular field clues of greater accuracy are provided by the disparity of the retinal images seen by the two eyes and the effort expended in convergence, while in Placentals in which the eyes are coordinated physiological diplopia probably becomes a potent factor in stereopsis for near objects, together with parallactic localization of an object in space.

That uniocular clues do play a considerable part in spatial perceptions in animals is obvious from the visual judgments formed by many animals with panoramic vision, and is confirmed by several observations. We have already noted the jerky or oscillatory movements of the head so constantly seen in many birds; viewing space

in this way from a succession of angles in rapid succession, parallax observations must be made providing a basis for the estimation of distance and relief ; in this rapid process the simultaneous parallax clues of binocular vision are replaced by the successive clues of unioocular vision. It was stressed by Grinnell (1921) that before pecking their food birds adopt the similar habit of "rapid peering"—cocking their heads now to one side and now to the other to view the grain or the berry from different aspects and localizing it against the background from different angles. The pendular head movements of snakes and the nodding of many types of lizards probably come into the same category. It was found by Benner (1938), for example, that one-eyed chicks peck as accurately as two-eyed specimens, relying (presumably) largely on unioocular parallax for the accuracy of their judgments of distances. The importance of shadow-effects was also brought out by Benner ; if the seed-grains were illuminated in such a way that their shadows were eliminated, his chicks neglected them, while painted representations of shadowed grains deceived them. The judgments of distances possible by unioocular vision may, indeed, be of extreme accuracy. We have already commented on the deft way in which the chameleon, suddenly converging both eyes upon an insect, captures it without fail with its long tongue ; while ordinarily both foveæ seem to be employed in this action, nevertheless Canella (1936) found that after the loss of an eye it could catch its prey with the same infallibility, retaining while so handicapped its accurate evaluation of three-dimensional space.

Binocularity, however, with the possibility of stereopsis must add considerably to the animal's appreciation of space and its judgment of distances, particularly near at hand. That such judgments are often good and occasionally superb is obvious from the many instances of behaviour that could be cited. The extraordinary agility of small FISHES darting rapidly up a shallow stream so quickly as almost to escape human observation and at the same time avoiding all obstacles, provides a good example of the excellent judgment of distances possible in some species. The schooling behaviour of many species induces fine visual judgments : vast aggregations of fish, both fresh-water and marine, wherein each individual maintains its position alongside its neighbours retaining a constant distance between each other like ranks of soldiers on parade can only be based on extremely precise visual orientations (Morrow, 1948 ; Gudger, 1949) (Fig. S47).

The judgments of size by certain fishes is exemplified by their response to visual illusions. Herter (1930) found that the response to such illusions was the same as in human beings ; fish trained to feed from the larger of two black circles chose the left-hand circle in Fig. S48. The astonishing visual accuracy of the archer-fish, *Toxotes*



Toxotes jaculator

jaculator, has frequently been quoted to illustrate how highly developed the judgment of distances may be in a fish ; while swimming it will spit a jet of water at an insect flying three feet above the surface with an astonishing accuracy, overwhelming it in the air and devouring it when it has been brought down to the surface of the water. An animal, particularly one not provided with a fovea, which can overcome the visual disabilities of localization in air while immersed in water ¹



FIG. 847.—THE SPATIAL ORIENTATION OF FISHES.

Resting trout lying in the Brule River, Minnesota. Note their arrangement in regular and disciplined ranks (Gudger ; from Thorpe's *Learning and Instinct in Animals*, Methuen and Co.).

and can still so deftly impale a flying insect must have an unusually excellent judgment of distances.

Similarly in AMPHIBIANS and REPTILES, the accuracy of the insect-catching activities of the frog, the toad or the lizard betoken well-developed spatial judgments ; but in some BIRDS this faculty appears to be even of a higher standard. This particularly applies to birds of prey, which swoop down on their quarry with unerring accuracy from astonishing heights, a feat doubtless rendered possible by the bi-temporal foveæ. The accuracy of the hawk, provided with two temporal foveæ, in swooping on its prey upon the ground at great speed and with great precision is in strong contrast to the conduct of

¹ p. 672.

a bird such as the gannet, *Sula bassana*, which is provided only with laterally directed central foveæ, and feeds by diving for fish. Portier (1923) found that if he fastened fish to floating pieces of wood the birds dived for them with great directional accuracy but, misjudging the distance, impaled their open beaks in the wood, a lack of precision which would bear no penalty were the fish swimming freely in the yielding water.



Gannet

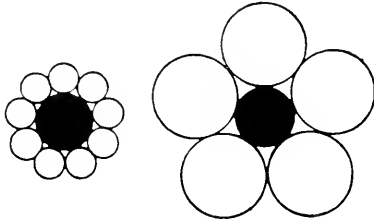


FIG. 848.—VISUAL ILLUSIONS WITH CIRCULAR FIGURES USED IN TRAINING OF FISH.

The black circle surrounded by small circles appears larger than a circle of the same size surrounded by larger circles (after Herter, 1930).

It is interesting that the visual judgment of birds is subject to the same illusions as ours, showing its basic similarity on the perceptual level. Thus Révész (1924-25) showed that hens and chicks trained to peck for the smaller of two figures (rectangles, squares, circles, etc.) when presented with two drawings illustrating the Jastrow illusion, pecked preferentially from the upper (Fig. 849). Similarly in experiments with doves (Warden and Baar, 1929) and with chicks

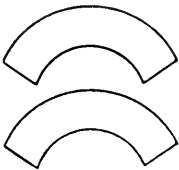


FIG. 849.—THE "JASTROW" ILLUSION.

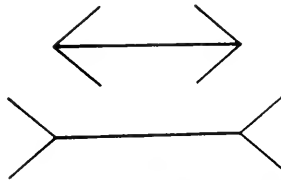


FIG. 850.—THE "MÜLLER-LYER" ILLUSION.

(Winslow, 1933) it has been shown that their response to the Müller-Lyer illusion was comparable with that of the human being (Fig. 850). It would seem, therefore, that the form as a whole impresses itself on the consciousness of the bird, thus providing evidence for the Gestalt theory of perception. The rapid assessment and recognition of a territory of the homing bird seems to be another example of the same process (Thorpe, 1944; von Haartmann, 1949; Fabricius, 1951; Wilkinson, 1952; and others); so also is the curious phenomenon of

"imprinting" whereby a newly hatched fledgling attaches itself to the first thing it sees, usually its parent, sometimes a bird of another species, occasionally a human being,¹ or experimentally in incubated birds to an inanimate object (Lorenz, 1935 ; Alley and Boyd, 1950 ; Ramsay, 1950 ; and others).

Among PLACENTALS the accuracy of visual judgments varies. In most of the lower nocturnal types it is of low degree ; thus Greenhut and Young (1953), in assessing the accuracy of jumps by rats, found that they appeared to have little or no visual perception of distance ; little difference was found between the performances of normal, hooded or albino animals. On the other hand, the agility of the arboreal Placentals, the accuracy of the larger Felidae in leaping on their prey, or the sure-footedness of the swifter Ungulates in galloping or jumping over rough country is testimony that accurate spatial judgments are not a monopoly of the Primates.

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¹ This phenomenon was known to Pliny (*Nat. Hist.*, **10**, 37).

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THE PERCEPTION OF MOVEMENT

From the biological point of view the two critical functions of vision are the control of the movements of the individual and the perception of the movement of objects in the outside world ; it is for this reason that eyes are found essentially in actively moving animals while in those leading a sedentary existence they degenerate.¹ The fundamental visual sensations are therefore the perception of light and of motion ; the perception of form and of colour are accessory. In the human eye the latter two are essentially the prerogative of the recently evolved central area and the periphery of the retina is primarily concerned with the former; so in the wide panoramic field of the lower Vertebrates the perception of movement is the most important aspect of the animal's visual experience. Even in creatures so lowly as the larvæ of *Ambystoma*, Moore and Welch (1940) obtained an association by training between food and movement or between food and light, and experimenting on the frog, *Hyla*, Pache (1932) found that recognition of forms such as triangles, circles or crosses depended essentially on the occurrence of some movement. It is well known that Amphibians such as the frog or Reptiles such as turtles, lizards and snakes appear not to see motionless prey, just as the rabbit in flight will collide with a motionless man. The eyes of the lower Mammals can see little else beyond light and movement, while Schmid (1936), studying the visual performance of the dog, concluded that the recognition of a moving object was possible at a much greater distance than of the same object when stationary (900 compared with 585 metres).

From the physiological point of view the perception of movement depends on two factors—the fineness of the retinal mosaic and the persistence-time of vision. When the visual elements are few the retinal area served by a single optic nerve fibre is large ; in such a “ coarse-grained ” retina an image must travel a considerable distance before it excites the sensory elements associated with another optic nerve fibre so that a small movement may not be appreciated. Similarly, if the physiological effect of stimulation persists for a long time,

¹ p. 721

a retinal element, once stimulated, cannot react quickly to a new stimulus; an image moving across such a retina will therefore appear as a blurred streak and not as a clearly defined pattern. The persistence-time can be studied by the well-known method of flicker, and can also be determined objectively by studying the electrical reactions of the retina to intermittent stimulation. We have already seen that great differences exist in this respect between the "fast eyes" of swiftly moving diurnal insects and the "slow eyes" of more sluggish nocturnal types. Similarly among Vertebrates the persistence-time is shortest in rapidly moving animals of diurnal habit. Both a fine retinal "grain" and a short persistence-time are therefore associated with the mechanism required for good visual acuity and the appreciation of movement.

The limits of the perception of movement in Vertebrates have not received much study. Boulet (1953-54) found that if several perch (*Perca fluviatilis*) were confronted by a moving sphere in controlled conditions to excite the optomotor reaction, half the fish responded with eye movements when the angular velocity was 12° per sec., and all of them when it was between 14° and 26° per sec.; movements quicker than 78° per sec. excited no response and were probably not perceived as such. This compares poorly with the performance of the human fovea where the minimum angular displacement perceived is from 6 to 10 secs. of arc and the upper perceivable limit of speed corresponds to an angular velocity between 140° and 350° per sec.

The perception of movement is, of course, only relative. Beebe (1934) brought this out well by his observations on the conduct of fish in his oceanographic studies. When standing on the ocean floor, so long as he stood motionless and erect he excited the attention and curiosity of the surrounding fish, but if he rocked and swayed with the current in keeping with the weeds of the sea-bottom, they paid no attention to him and appeared not to see him.

Animals appreciate STROBOSCOPIC MOVEMENT in much the same way as we do. Thus Gaffron (1934) found that if fish were contained in a tank surrounded by a revolving striped drum illuminated intermittently, they reacted as if the drum were stationary or were turning in the actual direction of motion or in the opposite direction depending on the frequency of the illuminating light, the response of the fish being precisely similar to her own (Gaffron's). Similarly, von Schiller (1934), having trained the minnow, *Phoxinus*, to respond positively to the upward movement of a white square at a definite speed in feeding experiments, found that the same response could be elicited if two squares were successively illuminated at time-intervals such that the stroboscopic movement thus appreciated corresponded to the real movement in the initial experiment. In this connection Walls (1942) pointed out that the interest of the dog in motion pictures and its complete indifference to still pictures is a demonstration that to it also an appreciation of apparent movement corresponding to that of man is a real perceptual experience.

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Boulet. *C. R. Soc. Biol. (Paris)*, **147**, 1623 (1953); **148**, 583 (1954).
Gaffron. *Z. vergl. Physiol.*, **20**, 299 (1934).
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PART IV
EVOLUTIONARY BY-WAYS

MEDIAN EYES

RUDIMENTARY EYES

LUMINOUS ORGANS

ELECTRIC ORGANS



FIG. 851.—RENÉ DESCARTES (1596–1650).

CHAPTER XIX

MEDIAN EYES

WE have already seen¹ that it is not unusual for the region of the mid-brain (diencephalon) of certain Vertebrates—and particularly the ependymal cells lining the posterior portion of the first embryonic vesicle which persists as the third ventricle of the brain—to show evidences of an optical as well as a glandular function. From this region the optic vesicles which form the lateral eyes emerge as out-pouchings; from the floor is derived the neural portion of the pituitary gland; in the ventral area are nuclei of internal secretion²; and from the thin roof is given off the pineal

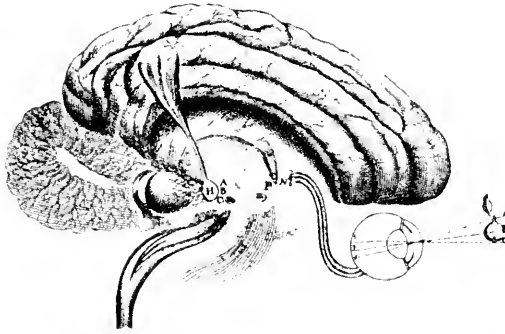


FIG. 852.—DESCARTES'S ORIGINAL DIAGRAM ILLUSTRATING THE EFFECT OF LIGHT UPON THE RATIONAL SOUL LYING IN THE PINEAL GLAND (from a photograph by Prof. J. F. Fulton).

apparatus (or epiphysis), which, although usually glandular in function, becomes differentiated into a median eye in some species. This dorsal up-growth of the roof of the diencephalon is represented in varying degrees in all Vertebrates with the exception that the pineal process is absent in the dugong (*Halicore*), a decadent and sluggish sea-cow, and in whales (Cetaceans), while the pineal body is absent in the armadillo (*Dasypus*) and in the dolphin (*Delphinus*).

The significance of the pineal body has always been an enigma. The ancient Romans described it as the *glandula pinealis* and by such anatomists as William Cooper (1666-1709) and Jacob Henle (1809-1885) it was considered as a lymphatic "gland." In the more speculative philosophy of René Descartes the body was a machine directed by a "rational soul" which dwelt in the pineal gland. This conception, sarcastically derided by Voltaire, is illustrated in Fig. 852, taken from Descartes's work *De homine figuris et latinitate donatus a Florentio Schuyt* (Leyden,

¹ p. 537.

² p. 557.

1662), which demonstrates figuratively the effect of light upon the soul lying within the gland.

It is impossible to overestimate the influence of RENÉ DESCARTES (1596–1650), the great French philosopher, on the development of European thought. In contradistinction to Francis Bacon, the great empiricist who based his philosophy on observed facts, he disregarded the role of experimentation and sought to build a mechanical conception of the universe on mathematical principles. In pure mathematics, he invented coordinate geometry, making it algebraic, and developed the conception that mass and time were dimensions as fundamental as those of space. Finding the intellectual atmosphere of France unsympathetic, he went to Holland

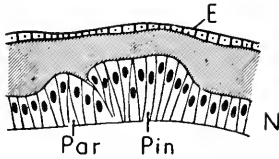


FIG. 853.

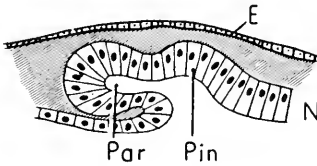


FIG. 854.

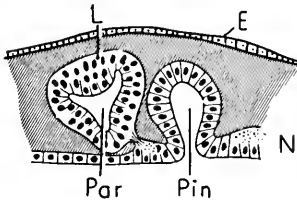


FIG. 855.

FIGS. 853 TO 855.—THE DEVELOPMENT OF THE MEDIAN EYE IN THE EMBRYO OF A LIZARD, *LACERTA*.

Medial sections through the roof of the diencephalon showing the development of the pineal and parietal organs. Fig. 853 in an embryo of 3 mm.; Fig. 854, 5 mm.; and Fig. 855, 7 mm.

E, epidermis; *N*, neural ectoderm of the roof of the diencephalon. The hatched area represents mesoderm. *Pin*, the anlage of the pineal organ; *Par*, the anlage of the parietal organ; *L*, the anlage of the lens (after Novikoff).

(1628) and there published his two great works, the *Discourse on Method* (1637) and the *Principles of Philosophy* (1644), both of which were placed on the list of prohibited books in Rome and Paris (1663). Rejecting the classical view of his time derived from Aristotle that nature was a single system hierarchically ordered with a Deity at the apex, he reasoned that the material universe was a homogeneous mechanical system composed of qualitatively similar activities following quantitative mechanical laws susceptible to mathematical analysis. Alongside this machine-world which included the human body, animals, plants and inorganic nature, there was a spiritual world in which the body of man alone of all material things participated by virtue of his soul. Ever since his time this dualism of the Cartesian philosophy has permeated European thought; and although to us today the designation of the pineal body as the meeting place of the two worlds may seem speculative and fanciful, it must be admitted that regarding the function of this organ our ideas are still as nebulous.

In its most elaborate form the pineal apparatus consists of two parts which arise from the middle of the epiphyseal arch, the most posterior of

the three arches of the roof of the diencephalon—a PINEAL ORGAN or EPIPHYSIS¹ lying more posteriorly and a PARIETAL or PARAPINEAL ORGAN lying more anteriorly, sometimes arising in association with the pineal body, but sometimes independently of it. The former is connected with the posterior commissure; the latter with the superior (habenular) commissure; their development in the embryo of the lizard (*Lacerta*) is seen in Figs. 853–5). The pineal body is connected nervously with the right habenular ganglion, the parietal with the left, suggesting that originally they may have been right and left members of a pair.

The highest development of a median eye is seen in the most primitive Vertebrates, the CYCLOSTOMES (Fig. 856). The lamprey (*Petromyzon*) is provided with both a pineal and a parietal organ having the structure of an eye with a considerable degree of retinal differentiation (Fig. 864); but in Myxinoidea no trace of either is seen. The presence of an impression in the mid-line of the roof of the cranial cavity in fossil remains of the closely-related Agnatha (*Pteraspis*, *Cephalaspis*)—the oldest known Vertebrates—is an indication of the occurrence of a pineal organ in these very primitive types, and since the impression is often duplicated the presumption is that the median eye at this stage in evolution was paired (Gaskell, 1908; Woodward, 1922; Heintz, 1932; Hills, 1933).

Among FISHES certain old-fashioned ganoid types retain a relatively well-developed median eye somewhat resembling the parietal eye of Cyclostomes. In the sturgeon, *Acipenser*, in addition to supporting cells of ependymal character, the vesicle contains many cells of a sensory type with ganglion cells and efferent nerve fibres; the structure thus resembles the parietal sense-organ rather than a secretory gland. A somewhat similar organ is seen in the primitive fish, *Polypterus*, found in African rivers, and the Holostean, *Amia* (Hill, 1894; and others). In Selachians (skate, shark, dogfish, etc.) the pineal body is set on a long stalk and often perforates the skull through a pineal foramen to appear beneath the skin as a closed vesicle (Fig. 857); alternatively it may lie within the skull in a recess in its cartilaginous roof (Holocephali). In these fishes the eye-structure has disappeared, the vesicle is small and consists of ependymal cells, and the tendency is probably towards glandular formation (Cattie, 1882; Locy, 1894). In Teleosteans (trout, salmon, pike, herring, etc.) the pineal apparatus is not so well developed, and is somewhat variable; in contrast to "ganoid" and cartilaginous fishes, the vesicle tends to be large and the stalk short. In these bony fishes it rarely reaches the under-surface of the skull, and although it contains cells of neural and glial character among the ependymal cells, it never shows a developed ocular structure. It is interesting, however, that in this class of fishes the superficial

¹ Galen (c. A.D. 130–200) used the non-committal, topographical Greek term—ἐπί, upon, φύσις, growth; the Latin term is descriptive of the shape—*pinus*, a fir-cone. The term "epiphysis" is usually applied to the deeply situated glandular organ seen in Mammals in contrast to the sensory "pineal eye" of the lamprey or *Sphenodon*.

structures, including the skull, are sometimes transparent while occasionally the degree of opacity of the integument is regulated by chromatophores (Breder and Rasquin, 1950). In some cases (the trout, *Salmo trutta*) a smaller off-shoot from the roof of the diencephalon may perhaps represent a vestigial parietal organ. In the lung-fishes (Dipnoi) the pineal apparatus is degenerate and makes no attempt to reach the surface or assume a sensory structure.

FIGS. 856 TO 859.—THE PINEAL AND PARIETAL ORGANS IN VERTEBRATES.

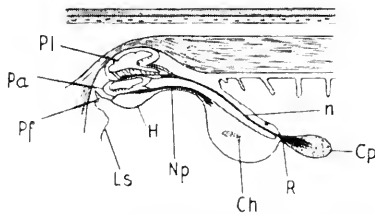


FIG. 856.—In Cyclostomes (the lamprey).

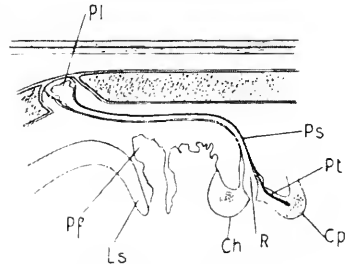


FIG. 857.—In Selachians.

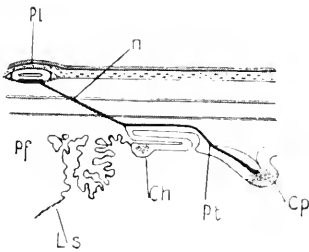


FIG. 858.—In Amphibians.

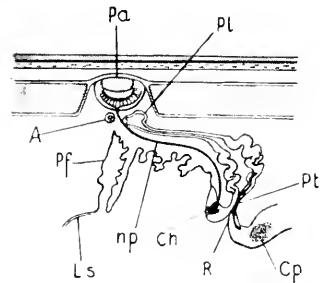


FIG. 859.—In Reptiles (*Sphenodon*).

A, accessory parietal body ; *Ch*, habenular commissure ; *Cp*, posterior commissure ; *H*, habenular ganglion ; *Ls*, lamina terminalis ; *n*, pineal nerve ; *np*, parietal nerve ; *Pa*, parietal organ ; *Pf*, parafysis ; *Pl*, pineal organ ; *Ps*, pineal stalk ; *Pt*, pineal tract ; *R*, pineal recess (after Tilney).

Among AMPHIBIANS, the primitive tailed class, Urodela (salamanders, newts, *Ambystoma*, *Proteus*, etc.), possesses a very rudimentary pineal organ, but the occasional possession of pigment granules (the olm, *Proteus*) and even of some nerve fibres suggests some affinity with a photosensitive structure. In the degenerate blind and limbless Cæcilians (Apoda) the pineal organ is similarly degenerate. In the tailless Amphibians (Anura), however, it is more fully represented in the early stages of development. Thus in the young frog (*Rana*) the pineal body comes to the surface above the skull as an eye-structure, its position being indicated by a pale area where the cutaneous pigment and glands are scanty or absent, but it

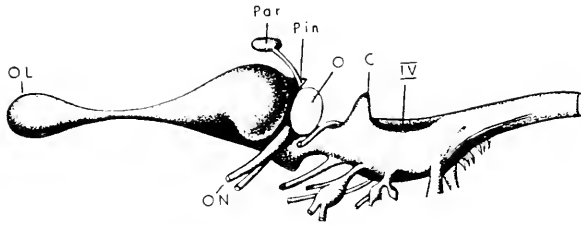


FIG. S60.—THE PARIETAL AND PINEAL BODIES OF *SPHENODON PUNCTATUS*.

A lateral view of the brain. C, cerebellum; O, optic lobe; OL, olfactory lobe; ON, optic nerves; Par, parietal eye; Pin, pineal body (epiphysis); IV, fourth ventricle. The structures issuing below are the cranial nerves, III to XII.

degenerates and disappears in adolescence leaving a rudiment of an eye connected by a nerve with the posterior commissure (Fig. S58) (Leydig, 1891; Braem, 1898; and others).

In the primitive REPTILES the eye-structure reaches its highest development in the parietal organ (Figs. S59–S60); in the New Zealand tuatara (*Sphenodon*), for example, it passes through the skull by a “parietal foramen” and lies beneath the skin, the scales of which become specialized and transparent in this region. In this animal as well as in some other types, an ACCESSORY PARIETAL ORGAN lies contiguously; it is variable in structure, vesicular or solid, and tends to disappear with maturity. In lizards such as *Lacerta*, the arboreal lizard, *Iguana*, and the slow-worm, *Anguis* (a limbless lizard), the parietal eye loses connection entirely with the pineal body and



FIG. S61.—THE PINEAL GLAND IN MAN (from Gladstone and Wakeley, *The Pineal Organ*).

has an independent parietal nerve associated with a near by parietal centre, a connection which in many cases is transitory and degenerates before maturity so that the organ would appear to lose its function. In these species the pineal body is always rudimentary and the vesicle is usually absent. It is also interesting that the presence of a parietal opening in the roof of the skull of fossil labyrinthodont amphibians and extinct reptiles of the Palaeozoic and Mesozoic eras suggests that a functional eye existed in these species also. In the more recent reptiles, such as geckos, snakes, tortoises, turtles, crocodiles, and alligators, the eye-structure disappears and the epiphyseal arch gives rise to a glandular organ, an arrangement retained in the higher animals. In some birds and mammals analogous rudiments

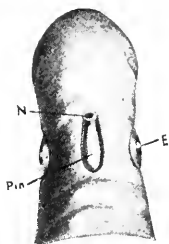


FIG. 862.—THE LAMPREY, *PETROMYZON*.

Dorsal view of the head end of the animal showing the eye, *E*, the nasal aperture, *N*, and the pineal area, *Pin*.

appear in embryonic life which disappear with development,¹ but in these types the pineal organ has a glandular structure and lies snugly hidden on the roof of the diencephalon between the cerebrum and the cerebellum (Fig. 861). It is thus evident that the pineal organ constitutes a definitive eye only in the lamprey and to a less extent in certain primitive "ganoid" fishes, while the parietal organ forms an eye-like structure in the lamprey and also in primitive reptiles; otherwise the latter organ is vestigial.

THE MEDIAN EYE OF THE LAMPREY lies under a localized area of transparent skin on the midline of the dorsal surface of the head immediately behind the single median nostril (Fig. 862). It consists of two diverticula lying vertically one upon the other (Ahlborn, 1883; Beard, 1889; Stúdnicka, 1905; Dendy, 1907; Mygind, 1949). The more superficial and dorsal vesicle is the pineal, the lower the parietal eye (Fig. 856). Together they form an organ incapable of optical imagery but doubtless able to appreciate differences in light intensity. Of the two the pineal eye is the more elaborately developed (Figs. 863 and 864). It forms a vesicle lying directly underneath the skin; the cells of the superficial wall are elongated to form a flat and imperfect lens; those of the deeper wall form a pigmented retina comprised of sensory and supporting cells, ganglion cells and nerve fibres which pass as the pineal nerve in the posterior commissure to the right habenular ganglion. The retinal pigment is of two types—a dark melanin-like pigment and whitish-yellow granules corresponding closely to the guanine-like pigment of the skin; the first has an absorbent, the second probably a reflective function analogous to the similar pigment in the compound eyes of some Arthropods. The free ends of the sensory cells face the lumen of the vesicle which is filled with a nucleated syncytial "vitreous." The parietal organ forms a somewhat similar vesicle of simpler construction, varying considerably in size; the rudimentary parietal nerve leads through the habenular commissure to the left habenular ganglion.

THE MEDIAN EYE OF LIZARDS and *Sphenodon*² is derived from the parietal body and forms a remarkably eye-like organ (Spencer, 1886; Leydig, 1887; Strahl and Martin, 1888; Klineckowström, 1893; Virchow, 1901; Stúdnicka, 1905; Dendy,

¹ Pigeon (Livini, 1905), guinea-pig (Chiarugi, 1919), ox (Favaro, 1904).

² p. 379.

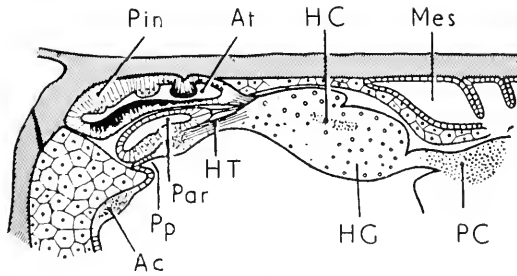


FIG. S63.—THE MEDIAN EYE IN THE AMMOCETE OF THE LAMPREY, *PETROMYZON*.

Longitudinal section through the roof of the fore- and mid-brain. *AC*, anterior commissure; *At*, atrium of the pineal organ; *HC*, habenular commissure; *HG*, habenular ganglion; *HT*, habenular tract; *Mes*, mesencephalon; *Par*, parietal organ; *Pin*, pineal organ; *PC*, posterior commissure; *Pp*, paraphysis (after Stúdnicka).



FIG. S64.—THE MEDIAN EYE OF *LAMPETRA FLUVIATILIS*.

Section through the head of the animal showing the two vesicular-like structures in the centre of the figure, the pineal and parietal bodies, lying in the ventricle underneath a relatively transparent area of skin and subcutaneous tissue. The two solid masses in the lower portion of the picture represent parts of the brain (Mallory's phospho-tungstic acid haematoxylin) ($\times 24$) (Katharine Tansley).

1907-11; Nowikoff, 1910; Gasson, 1947; Trost, 1953). It is situated in the parietal foramen of the cranial roof immediately under the integument and is covered by a specially modified scale where the black pigment is absent and the green is only feebly represented so that it is relatively transparent (Fig. 459). The eye takes the form of a flattened vesicle lying in a connective tissue capsule; the cells of the distal wall are elongated to form a lens which sometimes contains a central pigmented area; the cells of the proximal wall are differentiated to form a retina (Fig. S65). In some types such as the American "chameleon", *Anolis*, the latter is relatively crude but usually there is a reasonably well-differentiated sensory layer composed of visual and

intercalary cells, the latter being pigmented except in *Sphenodon* in which the pigment is extracellular. In the lizards this pigment shows adaptive changes, moving towards the sensory terminations of the cells on exposure to light (Nowikoff, 1910). Peripheral to the visual cells lies a layer of bipolar ganglion cells, the nerve fibres issuing from which form the parietal nerve which runs down the parietal stalk either to the right (*Anguis*, *Lacerta*) or left (*Sphenodon*) habenular ganglion. The surfaces of the visual cells of the retina as well as those of the lenticular cells facing the cavity of the vesicle are richly provided with cilia; the cavity itself is filled with a delicate syncytium with a few oval nuclei enclosing spaces filled with fluid constituting a "vitreous."

It is to be noted that in all cases the surface ectoderm takes no part in the formation of the ocular vesicle, there is no secondary invagination, and the retinal cells are verted, resembling the eyes of Invertebrates rather than the paired lateral eyes of Vertebrates.

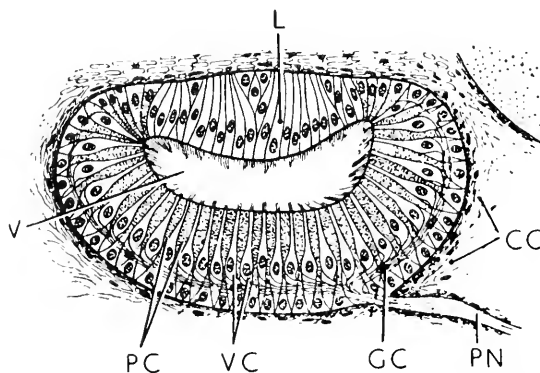


FIG. 865.—THE PARIETAL EYE OF THE SLOW-WORM, *ANGUIS FRAGILIS*.

CC, connective tissue; GC, ganglion cells; L, lens; PC, pigment cells; PN, parietal nerve; V, vitreous; VC, visual cells (after Nowikoff).

The function of the pineal organ in those species in which it assumes an ocular formation is undoubtedly optic although it would appear that it is confined to the directional appreciation of light and is incapable of optical imagery (Mygind, 1949). In those species wherein a glandular structure is evident, even among Mammals, the function of the pineal body is still obscure despite the considerable amount of research which has been devoted to the subject by morphologists, histologists, pathologists and clinicians. In man it reaches maturity between the ages of 6 and 7 years whereafter involutive phenomena begin to appear in the form of hyalinization, calcification and cystic formation (Rio-Hortega, 1922-29; Globus and Silber, 1931; and others). This involution after puberty together with the variations in the size of the organ observed during pregnancy, with sexual activity or after castration both in human subjects¹ and in animals,² have confirmed the clinical impression that its main association concerned skeletal growth and the sexual functions. It is to be remembered, however, that Pelizzi's (1910)

¹ Brandenburg (1929), Frada and Micale (1941).

² Santamarina and Venzke (1953).

classical syndrome of macrogenitosoma præcox has been reported as occurring in about 50% of cases in patients without pineal disturbances, while the majority of cases of pineal tumours do not exhibit sexual syndromes (Haldeman, 1927). It may even be that when these symptoms occur they may be caused by pressure on neighbouring structures such as the pituitary body and hypothalamus. The whole question of the existence of an endocrine secretion and what it may do is thus unsolved.

It is interesting that the association of the integumentary pigment with the visual system is maintained in some amphibians; thus pigmentary changes always occur in 10-day-old tadpoles if they are fed on pineal tissue (McCord and Allen, 1917), while the injection of pineal extract induces contraction of the melanophores of the African toad, *Xenopus* (Bors and Ralston, 1951).

The function of the parietal organ remained enigmatic until its eye-like structure in lizards was described by Leydig (1872) and confirmed in *Anguis fragilis* by De Graaf (1886) and in *Sphenodon* by Baldwin Spencer (1886). From these observations arose the view that the pineal apparatus is a primitive, unpaired, median, upward-looking eye, which has degenerated except in a few instances. It is more probable, however, that the hypothesis of Todaro (1888) is the more correct, that although often apparently unpaired, the organ is the result of the fusion of a pair (see Sterzi, 1912; Gladstone and Wakeley, 1940). The evidence derived from fossil remains of extinct Vertebrates, the duplication of the organ in primitive types, its occasional bifurcation in the higher species, and the frequent bilaterality of its nervous connections, is convincing. There is a strong case to be made that its primary function was sensory. In extinct fossil species it seems clear that a median eye coexisted with lateral eyes, olfactory organs and static organs, and the closure of the foramen in the roof of the cranium even in these early types indicates a regression of the organ and the loss of its visual function even in remote geological times, a tendency possibly due to the gradual predominance of the lateral eyes. Whether, as Patten (1890-1912) suggested, the pineal organ is linearly derived from the median eye of arthropods, particularly primitive arachnids, is a more debatable question.

On the other hand, the view has been put forward that its optical function is not essentially primitive but is rather the result of a secondary transformation, in which case the pineal body of Mammals cannot be looked upon as a vestigial and metamorphosed remnant of an eye. According to Tilney and Warren (1919) the histology of this region provides evidence that in all Vertebrates this portion of the brain possesses a pluripotential activity. Usually the fundamental tendency is in the direction of glandular formation, the secretion being contributed in a few cases to the cerebro-spinal fluid, but in most cases and in the Mammalia, to the blood stream as a hormone. In some species (Cyclostomes, Amphibians, and primitive Reptiles) the arch has become specialized with a visual function, an adaptive modification

answering the needs of the animal which in most cases is of sluggish habit with slow movements and a limited range of vision. In this view the two tendencies appear to run parallel rather than to be linearly derived. Which theory is correct must still remain a matter for discussion.

For the phylogeny of the pineal body, see the elaborate monograph of Gladstone and Wakeley (1940); its morphology and histology are well discussed in those of Stúdnicka (1905), Tilney and Warren (1919) and Rio-Hortega (1932); its physiological functions (as a gland of internal secretion) are fully noted by Kidd (1913), Schäfer (1926) and Bors and Ralston (1951); the vast clinical literature is found in Bailey and Jelliffe (1911), Boehm (1920), Laignel-Lavastine (1921), Horrax and Bailey (1925) and Calvet (1934); the veterinary literature in Santamarina and Venzke (1953).

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CHAPTER XX

RUDIMENTARY EYES

THE adoption of peculiar habits by a species of animal frequently stimulates the development of structural alterations suited to the unusual environment ; in a previous chapter we have discussed the many striking modifications adopted by the vertebrate eye to meet different conditions—aquatic or aerial vision, for example. Changes in the opposite sense may also occur when vision is no longer required, in which case the eyes may become rudimentary or vestigial or even disappear. The adoption of a sessile or sedentary habit involving sluggishness or quiescence so complete that light stimuli are valueless may lead to the development of a state of quasi or complete eyelessness in this way, but the more usual stimulus is a lightless habitat as in abyssal depths of the sea, dark caves, muddy rivers, burrows under the ground, or within the body of another animal.

A sharp distinction should be noted here between the permanent adoption of an environment wherein light is absent and the periodic adoption of *nocturnal habits* by many species for purposes of concealment or hunting—the daily use of caves by bats, for example, as opposed to permanent residence in a cave by cavernicolous fishes, or the use of a burrow as a home by the tuatara as opposed to the subterranean life of the mole. As a rule these nocturnal animals show the opposite tendency ; their eyes are elaborately developed to take every advantage of the dim illumination available, being often provided with a large lens, a wide pupil and a rod-retina.

This tendency for the structural recession and loss of function of an organ which is no longer biologically useful is not, of course, confined to the eye: the fate of the human appendix and coccyx are well-known examples of the regression of an organ, while the loss of its alimentary canal by the tapeworm or the possible reduction of a micro-organism to the bare bones of its nucleo-protein on the adoption of the habit of intracellular parasitism as a virus may be cited as examples of the complete disappearance of unnecessary characters. The biological mechanism of the transmission of such a disappearance, however, is not clear ; it is as if development has become arrested from lack of use. It is generally accepted that biologically useful characteristics tend to be retained in so far as they have survival value, but that those which are no longer useful should be purposely discarded as excess baggage is an expression of Lamarckian regression more positive than many would accept. Regression, however, does not necessarily imply degeneration as the term is generally understood. Darwin (1859) in his *Origin of Species* pointed out that both the use or disuse of an organ might equally lead to inherited changes both in plants and animals, and that parasites and “degenerate” creatures are as much a product of evolution as higher organisms ; they are as perfectly adapted to their restricted environment.¹

¹ The opposing argument used by August Weismann in his *Essay on Inheritance and Related Biological Questions* (1892) that successive generations of rats the tails of which had been cut off persisted in breeding rats with normal tails is inapposite since an artificial mutilation bears no biological relation to a purposive evolutionary regression. See Ray Lankester, *Degeneration, a Chapter in Darwinism* (1895) ; Demoor and others, *Evolution by Atrophy in Biology and Sociology* (1894) ; Vandervelde, *Parasitism, Organic and Social* (1895).

An alternative explanation is to suppose that there is an innate tendency for the eye to disappear which is normally opposed by natural selection because of its biological utility. It is doubtless true that a loss-mutation may become effective and the organ may disappear if its utility has ceased. It is to be remembered, however, that individuals may show a capacity for the eye to retrogress or develop according to its usefulness. Thus on the one hand, the eyes of larval cave-salamanders (*Proteus*, *Typhlotriton*) usually regress at metamorphosis, but will develop if the larvæ are grown artificially in the light (Kammerer, 1912); these sightless Amphibians thus appear to become blind in each successive generation. On the other hand, Ogneff (1911) found that if goldfish were kept in the dark for 3 years their eyes became degenerate and functionless while the eyes of many species of open-water fish become reduced if their biological value is lessened by increasing their food and eliminating predators from their environment.

We have already seen that ocular regression of this type may occur in most Invertebrates, particularly worms, Molluscs and Arthropods; the phenomenon is also encountered in all classes of Vertebrates with the exception of Birds. It is interesting that in most cases there is a corresponding increase in the development of other senses, such as the chemical, olfactory or tactile sense, which are of greater use than vision in dark surroundings.

THE SEDENTARY HABIT

A SEDENTARY HABIT may lead to the eyelessness in sessile forms. Thus among actively swimming Lamellibranchs such as the common scallop, *Pecten*, eyes of an extremely elaborate type are found, but in sluggish and quiescent forms they may be primitive, as in the bivalve, *Lima*, or absent as in the mussel, *Anodonta*. Among Crustaceans, those species of the Amphipod, *Gammarus*, which live in pools, or the Isopod, *Asellus*, which lives in holes is completely blind. In other species eyes may be present in the actively swimming nauplius stage, but when the adult becomes sessile these may become vestigial (the acorn-shell, *Balanus*, which encrusts rocks; the ship-barnacle, *Lepas*). We have already seen¹ that in insects the degree of ocular development is generally correlated with that of the wings (Kalmus, 1945).

THE ABYSSAL HABIT

AN ABYSSAL HABITAT renders eyes useless; for in the deep seas there is perpetual night. The transparency of the different seas varies greatly, a factor which depends largely on the concentration of plankton organisms, but at 370 metres in the Mediterranean and at 1,500 metres in mid-Atlantic there is not sufficient light to affect a photographic plate unless it is exposed for 2 hours; while the pelagic zone (down to 200 metres) is illuminated, the bathypelagic zone (200 to 2,000 metres) is thus very dark, and on the deep-sea floor (the benthonic zone), which may be several miles in depth, darkness is complete.

¹ p. 224.

It would seem, indeed, that all the inhabitants of this still, cold, dark world should tend to lose their eyes; possibly they would were it not for the development of luminous organs, a common acquisition by the inhabitants of the benthos.¹

Thus among abyssal Molluscs (*Chiton*, etc.) the eyes tend to degenerate even in Cephalopods wherein these organs are usually well marked; the only known blind Cephalopod, however, is *Cirrothauma murrayi*, an octopod which inhabits the N. Atlantic at depths of approximately 3,000 metres (Chun, 1911). Similarly among Crustaceans living at moderate depths, the arrangement of the pigment surrounding the ommatidia of the compound eyes remains permanently in the dark-adapted position, while in bathy-

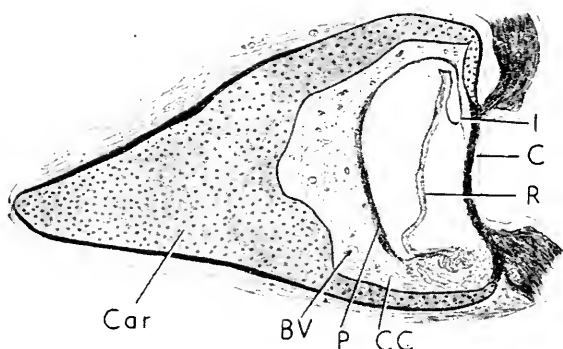


FIG. 866.—THE EYE OF A BLIND SELACHIAN FISH, *BENTHOBATIS*.

The ocular structures are of the most rudimentary type. *BV*, blood vessel; *C*, cornea; *Car*, cartilage; *CC*, connective tissue; *I*, iris; *P*, retinal pigment; *R*, retina (after Brauer).

pelagic types various stages of degeneration appear wherein all pigment is absent (*Cyclodorippe*)² or the ommatidia entirely disappear and the eye-stalks become fused with the carapace or are converted into tactile organs (*Cymonomus*, etc.) (Doflein, 1904). Paradoxically, side-by-side with species with degenerate eyes dwell other Crustaceans (shrimps, etc.) with fully developed and pigmented eyes, frequently, however, in creatures of a roving habit (Edwards and Bouvier, 1892).³ In general among bathypelagic fishes, species which penetrate to lower and lower depths develop progressively better eyes, adopting all possible expedients to improve their vision in dim illumination—a telescopic shape, an immense lens, a huge pupil, a brilliant tapetum, and a multiplication of the rods—until these organs become relatively larger than in any other Vertebrate. But below 500 metres in many instances the struggle is given up and the eyes shrink so that among the deeply benthonic fishes they are often vestigial and functionless or

¹ p. 736.

² p. 166.

³ Compare the "wondrous-eyed hopper" (Fig. 203), an inhabitant of the deep seas.

absent ; in this event it is interesting that some species maintain prociency by developing long filamentous " feelers " (the " feeler fish," *Bathypterois*). It is true that most of the inhabitants of the sea-bottom retain their eyes and that in some families these are neither unusually large nor small (such as the grenadiers, *Coryphænoididae*) ; it is also true that the only biological value of these visual organs is to catch the fitful gleams of luminescence ; but it is also true that many lose them (Alcock, 1902).

Thus among Selachians the eyes are vestigial in several families of the rays—*Typhlonarke*, *Bengalichthys* and *Benthobatis*. The eye of the last, for example, has a crude cornea, a rudimentary iris, an undifferentiated retina, and no lens (Fig. 866) (Brauer, 1908). Among Teleosts in some deeply bathypelagic forms such as *Saccopharynx* and *Cetomimus* the eye is vestigial. In the latter the oval globe is only 0.7 mm. in diameter, the lens and retina are rudimentary and the pigment epithelium unusually thick (Brauer, 1908). Among some benthonic Teleosts the eyes may be still more rudimentary and covered with opaque skin—*Barathronus*, *Typhlonus*, *Aphyonus*, and

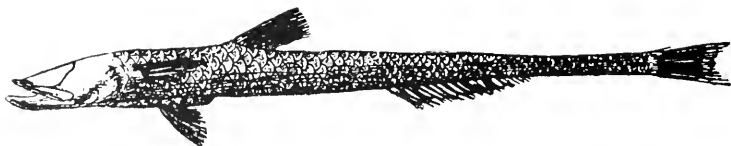


FIG. 867.—THE BLIND DEEP-SEA TELEOST, *IPNOPS AGASSIZI*.

Found at 2,000 m. ($\frac{1}{2}$ natural size) (after Garman, *Albatross Report*, 1899).

Tauredophidium. An inhabitant of the ocean floor, *Ipnops*,¹ is the only Vertebrate known to have no trace of eyes (Eigenmann, 1909) ; this is a small black fish with two luminous areas (resembling lanterns) in its head under the translucent bones of the skull where the eyes might be expected, possibly adaptations of these organs (Fig. 867).

THE CAVERNICOLOUS OR LIMICOLINE HABIT

A CAVERNICOLOUS OR LIMICOLINE HABIT, whereby life is spent in the darkness of caves or crevices or in a similarly lightless environment in mud or beneath stones, also leads to a tendency for ocular regression. This is seen among cave-dwelling worms such as the planarian *Kenkiidae*, or among Arthropods inhabiting a similar environment. In the latter phylum typical examples are seen in two species of Onychophores, *Peripatopsis alba* which lives in lightless caves, and *Typhloperipatus*, found under rocks ; in the cavernicolous beetle, *Anophthalmus*, which is possessed only of a dermal light sense (Marchal, 1910) ; the eyeless white cave-crayfish, *Cambarus ayersii*, which retains some light-sensitivity in its cerebral ganglion (Wells, 1952) ; and the cave-spiders (*Anthrobia*) which are entirely sightless ; but the phenomenon is most markedly seen in cave-dwelling Fishes and Amphibians.

¹ ἰπνός, a lantern ; ὤψ, eye.

Among Invertebrates with such degenerate eyes the Isopod *Typhlocirolana*—a small Crustacean found in a cave in the island of Majorca—may be taken as an example. The compound eyes are minute degenerate bodies $\frac{1}{3}$ mm. in diameter, without pigment in the ommatidia, while the crystalline cone and the proximal part of the retina are grossly atrophied (Menacho, 1913).

CAVE-FISHES¹ are all Teleosteans and it would seem probable that the ancestors of most of them can be traced from species in which a pre-adaptation to ocular regression had already been present owing to a previous existence in deep seas or muddy bottoms²; few of them (*e.g.*, catfishes of the genus, *Rhamdia*) have well-formed eyes; and some types (*e.g.*, the Mexican catfish, *Anoptichthys jordani*) show all grades of reduction of the eye from normal organs to rudimentary remnants. The latter are hatched with small but complete eyes, lacking, however, a circulation, and as the fish matures these gradually degenerate until all that is left in the adult is a most rudimentary organ lying deeply buried in a recognizable orbit associated with hypoplasia of the optic lobes (Gresser and Breder, 1940–41; Breder, 1942; Lüling, 1953–55; Kuhn and Kähling, 1954; Stefanilli, 1954). Some of the cave-fishes derive from deep-sea types such as the Brotulidæ which emigrated to the surface and there sought the darkness of crevices in reefs or caves. Three species have made the still more remarkable transition to fresh water—*Lucifuga* and *Stygicola* which are found in caves in Cuba, and *Typhlias* in Yucatan. Eigenmann (1909) concluded that these Cuban fishes initially inhabited caves in the coral beaches where they remained as these caves were elevated and became filled with and enlarged by fresh water; in his view the fishes are older than the island of Cuba. The eyes, which lie under the skin, are best developed before birth; thereafter they progressively degenerate until in old age they are represented by a shrivelled, pigmented vesicle, lying deeply in the large orbit, a process perhaps determined by a disturbance of the circulation. The bottom-grubbing catfishes which habitually shun the light are the ancestors of other types. These Siluroids which encyst themselves in the mud often have rudimentary eyes (Cope, 1864); thus the eye of the bull-head catfish, *Ameiurus*, has an ill-formed lens and a retina wherein the rods are large, the cones few and small, while the outer nuclear layer is represented by only two rows of nuclei, the inner by one, and the ganglion cells by a few widely-scattered elements.

The Amblyopsidæ, the North American group of cave-fishes characteristic of the caves of the Mississippi basin, are of considerable interest (Telkamp, 1844; Wyman, 1850–54; Kohl, 1892–93; Eigenmann, 1899–1909; Hubbs, 1938). They are

¹ A monograph by Carl H. Eigenmann, the Professor of Zoology of Indiana University gives a good account of the *Cave-Vertebrates of America* (Carnegie Inst., Washington, 1909), including a particularly illuminating and interesting study of the cave-fishes of the Mississippi Valley and Cuba. A subsequent monograph by Hubbs, *Fishes from the Caves of Yucatan* (Carnegie Inst. Wash., Pub. No. 491, pp. 261–295, 1938), lists all known blind fishes apart from deep-sea types.

² *Anoptichthys* is an exception in that it probably entered cave life as a stray and on losing its vision was constrained to remain.

negatively phototactic and if exposed in a well-lit pool will immediately seek refuge and hide under rocks. In *Amblyopsis* the eye lies deeply under the surface, the lens is vestigial or absent, the iris is represented by a pigment-free membrane and the retina contains only a few ill-formed cones. Similar rudimentary eyes are found in the two other related genera, *Typhlichthys* and *Troglichthys*; and in the only non-cavernicolous representative of this family, *Chologaster*, which inhabits the swamps of Kentucky and Tennessee, the eyes which lie under a patch of pigment-free epidermis are reduced rather than degenerate; the fish does not depend on its eyes, however,

for detecting or securing its prey or for avoiding obstacles. Although possessed of ears, experiments have shown that the sense of hearing of the Amblyopsidae is limited; the tactile sense is the one on which they rely to find and locate their food for which purpose they are provided with numerous tactile ridges principally in the region of the head (Eigenmann, 1909).

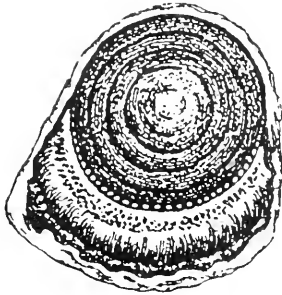


FIG. 868.—THE EYE OF THE GOBY FISH, *TRYPAUCHEN WAKERI*.

The eye is rudimentary and functionless (after Franz).

Some goby fishes (Gobiidae), particularly the "sleepers" living on muddy bottoms or in crevices, also have degenerate eyes. *Typhlogobius californiensis*, a blind fish which co-habits rocky crevices on the Californian coast with a blind species of shrimp on which it depends for food, has relatively normal eyes in the larval stage which become small, functionless and rudimentary in the adult, lying under the thick skin (Ritter, 1893); they lack tapetum, cones and vitreous, while, curiously, the lens may be either very large indeed or absent. It is as if a brave struggle were made to collect what light there is or, alternatively, the attempt has been abandoned.

Trypauchen and *Trypauchenophrys*, littoral crevice-dwellers in Japan, and other limicoline gobies as *Austrolethops*, and the sole, *Typhlachirus*, have similarly minute or rudimentary eyes (Fig. 868) (Franz, 1910-34). Undersized eyes are also usual in the fresh-water fishes which inhabit silty rivers such as are common in the great plains of America; only occasionally, as in Lake Balaton in Western Hungary, an immense shallow lake the waters of which are so turbid as to be virtually opaque, is an effort made to increase the sensitivity of the eye by the liberal deposition of guanine in an unusually well-developed tapetum (Wunder, 1926-30).

AMPHIBIANS. Amongst the Urodeles, the salamanders which live a secretive existence in shallow water, in caves, in mud and under flat stones, have little use for eyes. These organs are well differentiated in the larvæ but regress at metamorphosis (Zeller, 1888) (Fig. 869); as we have already



FIG. 869.—THE OLM, *PROTEUS ANGUINUS* (Zool. Soc., London).

FIGS. 870 AND 871.—THE EYE OF *PROTEUS ANGUINUS*.

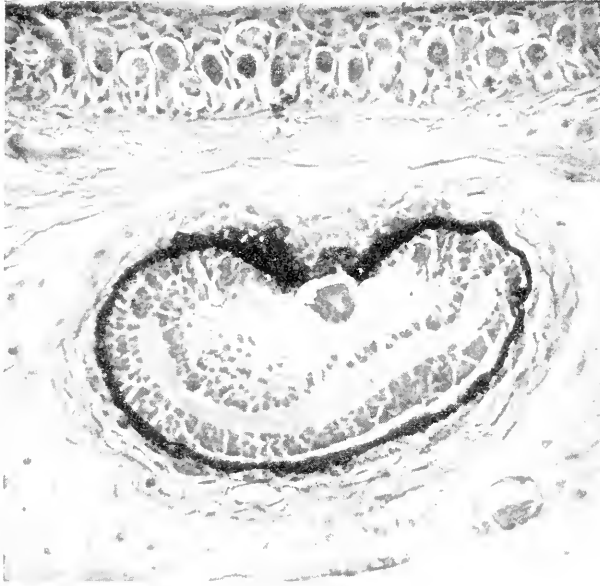


FIG. 870.—A vertical section through a rudimentary lateral eye in an animal of normal cavernicolous habit. The eye is seen to be a simple vesicle containing vitreous-like material centrally. It is surrounded by pigmentary epithelium and, owing to the absence of the lens, the lips of the optic cup meet at the distal aspect of the vesicle. The retina is unusually thick and relatively undifferentiated. The entire organ lies underneath the skin (E. F. Finckham).

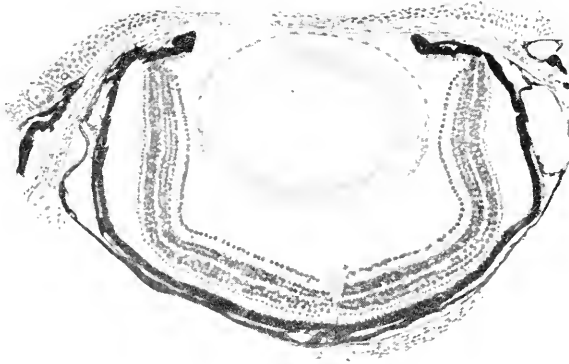


FIG. 871.—Meridional section through the eye of an animal kept in daylight. Note the presence of the ill-formed cornea, the well-formed lens and uveal tract, the hyaloid type of vascularization and the highly differentiated retina (after Kammerer).

noted, however, they may remain large and relatively well formed if development from the larval to the adult stage is artificially conducted in bright illumination (Kammerer, 1912) (Figs. 870-1). In natural conditions, however, they are concealed under the skin, microscopic and either capable merely of a directional light sense, as in limicoline types, or functionless, as in cave-living types. Other Urodeles, on the other hand, such as the newt (*Triturus*) or the North American axolotl, *Ambystoma*, have relatively simple but effective eyes, lacking iris folds and with a spherical lens, while in terrestrial salamanders the eyes, though small, are well formed.¹

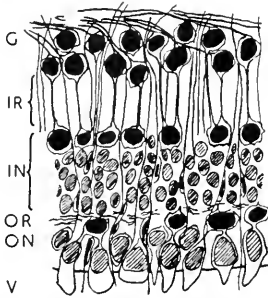


FIG. 872.—THE RETINA OF *PROTEUS ANGUINUS*.

G, ganglion cells; IN, inner nuclear layer; IR, inner reticular layer; ON, outer nuclear layer; OR, outer reticular layer; V, visual elements (after Kohl).

Among the cave forms the olm, *Proteus* may be taken as a typical example, several species of which inhabit the caves of Carinthia and Dalmatia (Fig. 869.) The eyes of the adult *Proteus anguinus* are minute spheres less than 0.5 mm. in diameter seen as shadows deep underneath the skin. They form simple vesicles without cornea or lens; originally a mere accumulation of epidermal cells within a capsule, the capsule disintegrates and the cells of the lens are replaced by connective tissue (Fig. 870). The ocular cavity is almost entirely taken up by a retina of a most rudimentary type and between it and the external epithelium lie the open remains of the optic vesicle. The visual cells are globular and bear no resemblance to rods or cones; there is an elementary nuclear layer and a reticular layer while the optic nerve is vestigial and largely neuroglial (Fig. 872) (Confogliachi and Rusconi, 1819; Desfosses, 1882; von Hess, 1889; Kohl, 1889-92; Benedetti, 1922; Stadtmüller, 1929).

Similarly rudimentary eyes, even more degenerate than those of their cavernicolous European relatives, are found in related types such as the American blind salamanders, *Typhlomolge*, inhabiting the underground streams of Texas, and *Haideotriton*; such eyes are functionless. The eyes of *Typhlotriton*, however, a salamander found in the caves of the Mississippi Valley, normal in the larva but degenerate in the adult, are more fully formed with a lens and a considerable degree of retinal differentiation although the rods and cones disappear in the fully grown animal; these constitute a link between the degenerate eyes of the Proteidæ and the normal urodelan eye (Eigenmann, 1909).

THE FOSSORIAL HABIT

The FOSSORIAL OR BURROWING HABIT has led to the regression of the eyes of many types of Invertebrates and Vertebrates.

Thus among worms which burrow on the land (*Lumbricus terrestris*) we have already seen that the visual organs are of a very primitive type,² while

¹ p. 346.

² p. 190.

those Polychætes which burrow in the sand or mud of the sea-shore may be without visual organs (the lob-worm, *Arenicola marina*)¹; sometimes the larval forms have eyes which disappear on reaching adulthood (Tampi, 1949). Similarly, sand-burrowing Molluscs may be unprovided with eyes (elephant's tooth shell, *Dentalium*).² Among Arthropods, those Myriapods which burrow in moist forest debris may lack eyes (*Pauropus*),³ as well as certain burrowing types of woodlice (Arcangeli, 1933). Among Insects the primitive minute Protura which burrow in moist soils impregnated with organic debris and are widely found in Europe, America and India, are without eyes, antennæ and wings; but the most interesting eyeless insects are termites and ants.

Termites (Isoptera), often mistakenly called "white ants," are widely found in Europe, Asia and Africa but are unrepresented in Great Britain;



FIG. 873.—TERMITE SOLDIER.



FIG. 874.—MALE DRIVER ANT.



FIG. 875.—FEMALE DRIVER ANT.

while they are extremely sensitive to light, most are blind and are completely without eyes (Fig. 873). They live in teeming millions in vast underground communities governed by a complex and efficient social system and alive with an immense and ordered business; nevertheless, blind and eyeless though they are, they conduct long regimented marches overland to seek and convey back the wood they eat, and the young alates temporarily develop wings in a frequently disastrous nuptial flight in the air.

Most ants (Formicidæ) have large and well-developed compound eyes but in some forms of Dorylinæ which dwell under the ground, eyes are lacking. The wandering ants (*Eciton*) of Central and South America show eyes in various stages of disappearance—small eyes without an optic nerve, orbital sockets without an eye, and so on—while the female driver ant (*Dorylus*) of Africa has no evidence of ocular or orbital remnants whatever. It is interesting and perhaps significant that in the latter species the winged male is possessed of eyes surpassing those of most insects, while all females, whether queen, fighter or worker, are blind (Figs. 874-5) (Maeterlinck, 1927-30; Marais, 1937).

It would seem probable that like all other members of the Hymenoptera (wasps, bees, etc.) all ants were originally sighted and it might seem logical that the underground types might tend to lose their eyes; but why the eyeless female should continue

¹ p. 191.

² p. 197.

³ p. 211.

to produce the fully-eyed male is not clear. Moreover, although their nest is underground, these ants are nomadic on the surface and their armies, the members of which are completely blind, are forever on the move. It is to be remembered that the big-eyed, innocuous male driver ant is a gentle and relatively useless creature—merely a stud animal with a momentary function as likely as not never to be fulfilled; while the monstrous regiment of his sisters ranks among the most ferocious and blood-thirsty creatures the world knows. It has been suggested that these unsexed females which march ahead against any obstacle and into any danger, which attack and devour anything alive in their line of march, would find difficulty in maintaining the iron discipline of their ranks if they were distracted by vision, and that blindness is therefore an asset of evolutionary value to the ferocious and purposive female but not to the idle and harmless male (Crompton, 1954). The suppression of eyes in this view (which many would not accept) is positive, differing entirely from the mechanism which usually induces eyelessness.

On the other hand, it may be that some other system of inter-communication exists of which we have no knowledge, outside the visible limits of the electromagnetic spectrum. It is indeed difficult to conceive how otherwise the extraordinarily complex activities within these underground cities could be conducted, not only as an ordered routine but with coordinated variations to meet unexpected emergencies of construction or war with equal facility, in which each member of the community—queen, king, soldier, policeman or worker—finds an appointed place. It may, indeed, be that eyes have become useless owing to the development of senses other, and perhaps more efficient, than our own.



FIG. 876.—*ICHTHYOPHIS*.

A subterranean burrowing Amphibian, limbless, somewhat resembling an earth-worm; the eyes are small, functionless and covered by skin (head on right).

Among Vertebrates, fossorial Amphibians, Reptiles and Mammals are encountered; in a sense some limicoline fishes (catfishes, etc.) which we have already discussed might be brought into this category.

Among Amphibians, the Cæcilians (Apoda) form a peculiar archaic group highly specialized for burrowing (Fig. 876)—*Cæcilia* of South America, *Ichthyophis* of Southern Asia, *Hypogeophis* of East Africa, *Siphonops* of America; with the exception of the aquatic *Typhlonectes*, all spend most of their lives underground. Their most efficient sensory organ is a retractile sensory tentacle situated at the anterior border of the orbit, while the eyes are very small (less than 1 mm.) and can be useful only in light-detection.

The minute eyes of the Cæcilians are attached to the skin and lie in a roomy orbit, largely filled by a Harderian gland which, however, is used to lubricate the sensory tentacle; the levator bulbi muscle of Amphibians is used as a compressor of this gland to assist in its evacuation. Two of the other extra-ocular muscles are commandeered to move the tentacle and have no action on the immobile eye, the retractor bulbi acting as a retractor of the tentacle and the internal rectus as a retractor of its sheath. The cornea is fused with the skin, there is no ciliary body or mesodermal iris, the lens is large, spherical and usually cloudy, while the retina is provided only

with simple but massive rods, and the two nuclear layers and the ganglion cells are represented by a few rows of sparse cells (Kohl, 1892; Hanke, 1912; Engelhardt, 1924).

Among Reptiles, burrowing snakes and lizards come into the same category. Within the group of snakes (Ophidia) the lowest types are the Typhlopidae, blind subterranean burrowers usually smaller than earthworms which occur in most of the warmer parts of the earth. The eyes are tiny and vestigial. It would seem that when the snakes originally went

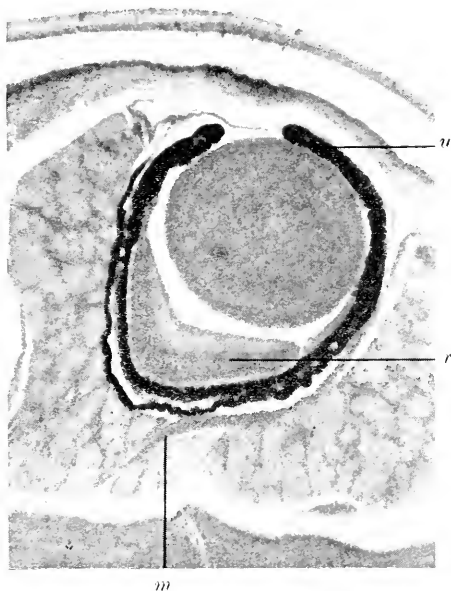


FIG. 877.—THE EYE AND ORBIT OF THE BLIND SNAKE, *TYPHLOPS*.

The globe is minute, less than 1 mm. in diameter. The heavily pigmented uvea, *u*, and the ill-formed retina, *r*, are well seen. Most of the cavity of the eye is taken up by the large lens. Anterior to this is the tenuous cornea, the enclosed conjunctival sac and the dermal "spectacle." *m* is a tenuous extra-ocular muscle (O'Day).

underground the eyes became vestigial, and when they again emerged from the ground the eye had to be reconstructed, but those of this primitive species retained their simple form (Walls, 1942)¹.

The eye of *Typhlops*, a blind snake widely distributed in the Southern Hemisphere and South East Europe, which lives on worms and insects obtained by burrowing, has a rudimentary uvea and a small embryonic cellular lens: the retina contains few and rudimentary visual cells and insignificant nuclear and ganglion-cell layers while a central area is lacking (Kohl, 1892) (Fig. 877). A similarly primitive eye is seen in *Typhlops lumbricalis*, a blind snake seen in the West Indies and Guiana (Muhse, 1903), and in the uropeltid snake, *Rhinophis* (Baumeister, 1908).

¹ p. 383.

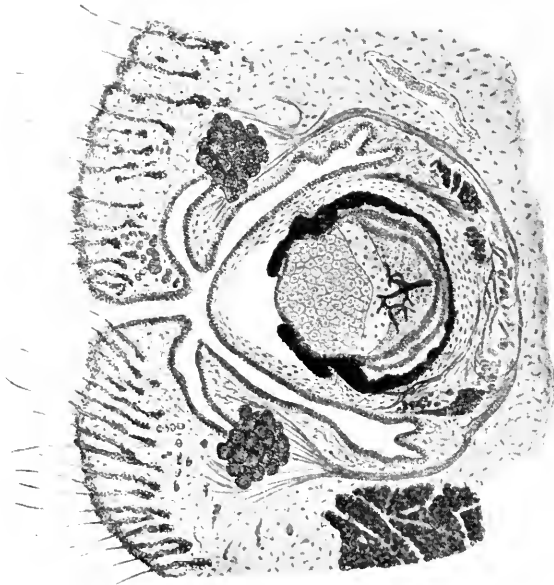


FIG. 878.—Section through the whole eye.

Note the pore-like opening in the lids, the elementary uvea, the cellular lens, and the hyaloid form of the central retinal artery (after Ciaccio).

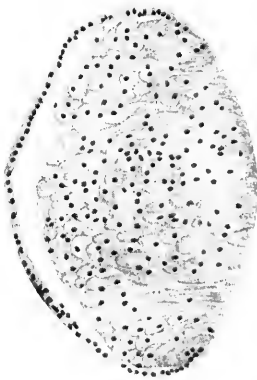


FIG. 879.—The lens.

Showing the immature cellular state and the persistence of the vesicle (after Rabl).

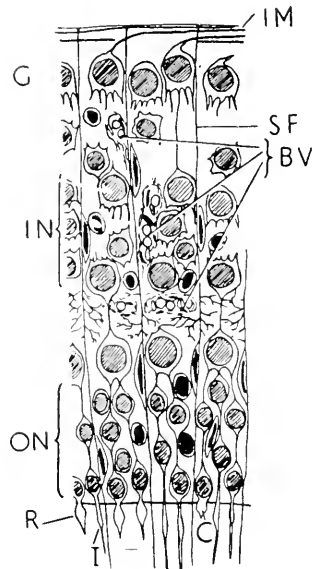


FIG. 880.—The retina.

The layering of the retina is relatively well-developed: *G*, ganglion cell layer; *IN*, inner nuclear layer; *ON*, outer nuclear layer. Blood vessels, *BV*, are seen in the inner layers and there is an external limiting membrane, an internal limiting membrane, *IM*, and nucleated supporting fibres, *SF*. Three types of visual cells are present: rods, *R*, cones, *C*, and "indifferent" elements, *I* (after Kohl).

Degenerate subterranean lizards (Amphisbænidæ), which are without limbs and almost without scales—such as the worm-like *Amphisbæna punctata* of Cuba or the similarly legless *Rhineura floridana* abundant in parts of Florida—have eyes equally minute buried beneath opaque skin, rarely consisting of more than a capsule of connective tissue enclosing an optic cup and a cellular lens without fibre-formation ; extra-ocular muscles and iris are lacking (Payne, 1906 ; Eigenmann, 1909). It is interesting that both in these snakes and in lizards, Harder's gland is many times larger than the eye.

Among Mammals a similar degeneration of the eye is seen in a small group of animals with burrowing habits which have led to a life of permanent darkness. These fossorial animals have little vision but an exquisitely developed sense of smell on which, indeed, most of them depend for their living ; the eyes are minute in size but relatively well differentiated, almost although not completely covered by skin to which they are adherent. In the common European mole only a minute pore, 0.1 mm. in diameter, is left in the skin through which little but the merest perception of light can be possible. In the blind mole of Southern Europe, *Talpa cæca*, this aperture is said to be usually lacking (Weber, 1904 ; Kazzander, 1921). In addition to the European moles, this group includes other Insectivores—the South African and Asian golden mole, *Chrysochloris* (Sweet, 1909), the American water-mole, *Scalops aquaticus* (Slonaker, 1902)—as well as the marsupial mole, *Notoryctes typhlops* (Sweet, 1909) and the rodent “ moles ” such as *Spalax*, and *Ellobius* which belong to the hamster branch of the mouse family.

The eye of the mole, *Talpa*, may be taken as typical, and appears as if it had ceased to progress from an early stage of embryological development (Lee, 1870 ; Ciaccio, 1884 ; von Hess, 1889 ; Kohl, 1892–95 ; C. Ritter, 1899 ; Henderson, 1952) (Figs. 878–9). The corneal epithelium may consist of a single layer of cells, the iris is small but present, and the choroid, unlike the mammalian but like earlier vertebrate types, has a single layer of vessels ; the lens is embryonic and cellular, while the central artery of the retina retains a hyaloid form and grows into the vitreous. In the retina, rods and cones are distinguishable and intermingled with them are cells of an intermediate type, but the normal layering of the mammalian retina is evident (Fig. 880). The non-neural parts of the eye are therefore particularly retarded, and it is interesting that Tusques (1954–55) found that their relatively normal development could be stimulated by large doses of thyroxine : the globe increased in size, the lids separated, the lens developed with the production of fibres and the entire organ began to take on the appearance of the eye of sighted animals.

THE PARASITIC HABIT

In most internal parasites the eyes are rudimentary or absent for the inside of an animal is as lightless an environment as any ; moreover, the sedentary life associated with parasitism can proceed in the absence of other activities so that, in addition to the recession of the visual organs, those of locomotion and often of digestion are reduced.

In the large number of endo-parasitic Invertebrates, eyes are lacking

or vestigial. Thus in the flukes (Trematodes) and in the round- or thread-worms (Nematodes) the eyes may be present in the freely-swimming larval stage but in the parasitic adult sense organs are limited to papillæ on the lips. In tape-worms (Cestodes) sense organs are lacking. Similarly eyes and other sense organs are not found in parasitic Crustaceans such as *Sacculina*, an organism parasitic on the abdomen of crabs. A similar example among Insects is provided by *Stylops*; the winged male has many ocelli but the minute female which is parasitic within bugs and bees is eyeless.



FIG. 881.—THE HAG-FISH, *MYXINE* (after Dean).

Among the Cyclostomes, the hag-fishes have rudimentary eyes which give no response to light. These small eel-like creatures live partly in the mud at the sea bottom and are partly voraciously parasitic within larger fishes. The glutinous hag, *Myxine*, with a wide distribution in the oceans, approaches more nearly than any other Vertebrate the condition of an internal parasite (Fig. 881); in other species such as the slime-hag, *Eptatretus* in the Southern Hemisphere and *Bdellostoma*, found in South African and Pacific waters, the eyes are not so degenerate (see Henckel, 1944). The eyes of the ecto-parasitic lamprey, on the other hand, are well-formed.¹

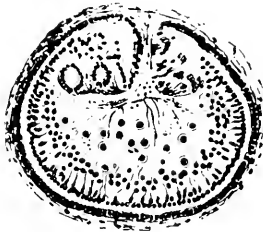


FIG. 882.—THE EYE OF THE HAG-FISH, *MYXINE GLUTINOSA*.

The eye is a simple vesicle almost entirely filled with poorly differentiated retina doubled over itself (after Dückler).

In *Myxine glutinosa*, the eyeball, about 0.5 mm. in diameter, is merely a simple vesicle lying in fat buried beneath the skin, almost entirely filled with a poorly differentiated retina doubled over upon itself (Fig. 882). Extra-ocular muscles, cornea, iris and ciliary body are unrecognizable, the sclera and choroid are undifferentiated, the lens is lacking, and there is no pigment either in the uvea or retina. The retina retains the form of the cavity of the optic vesicle, visual cells are not recognizable as such, layering of the retinal elements is crude and the optic nerve is vestigial (Kupffer, 1868; Kohl, 1892; Retzius, 1893; Allen, 1905; Eigenmann, 1909; and others).

It is noteworthy that although the eyes are functionless, a dermal sensitivity to light exists concentrated particularly in the head and cloacal regions and disappearing when the animal is skinned. There is a long latent period of about 20 secs. before the animal commences to swim and thereafter to burrow. The photochemical reaction is associated with vitamin A₁ and the response is mediated nervously through the spinal cord (Newth and Ross, 1955; Steven, 1955).

Endo-parasitic Fishes are rare, and the parasitic habit is not found among higher Vertebrates. The eel, *Simenichelys parasitica*, an inhabitant of deep seas and parasitic

¹ p. 263.

in halibut and other large fishes, has an eye covered by semi-opaque skin, but it is not rudimentary; nor are the minute eyes of the other parasitic Teleost, the pearl-fish, *Encheliophis jordani*, which spends much of its life inside the cloacae of sea-cucumbers.

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CHAPTER XXI

LUMINOUS ORGANS

THIS book opened with a discussion on the action of light upon living organisms ; a suitable postscript to this Volume is a passing (but not an exhaustive) reference to the opposite process—the production of light by organisms. Moreover, many luminous organs, although not homologous with eyes, have a structure so similar that a short description of the phenomenon of bioluminescence can hardly fail to interest the reader.

Bioluminescence is one of the most fascinating subjects in biology and it is not surprising that the emission of light by living creatures attracted attention from very early times. The luminescence of rotting vegetation and putrid flesh was known to Aristotle and classical writers such as Pliny wrote in detail of the phenomenon as seen in fungi on land and marine animals which are responsible for the phosphorescence of the sea. The early literature is full of delightful descriptions of the beauty of some of the observed phenomena, but modern work may be said to have begun with the French and Italian naturalists, A. de Quatrefages, whose classical works appeared between 1843 and 1862, and P. Panceri, whose observations were published between 1870 and 1878. It is interesting that Max Schultze, the great anatomist of Bonn, published a detailed account of the luminous organ of the fire-fly, *Lampyrus splendidula* (1865). More recently the researches of Raphael Dubois who published some 56 important papers between 1884 and the appearance of the masterly summary of his ideas on the production of animal light in Richet's *Dictionnaire de Physiologie* (1928), laid the foundations of our biochemical knowledge of the problem ; most of his classical work was done on the mollusc, *Pholas*, and from experiments on the elaterid

beetle he conceived the idea that the production of light was caused by the interaction between an oxidizable compound, luciferin, and an oxidizing enzyme, luciferase. In modern times the foundations laid by Dubois have been consolidated by the Dutch School associated particularly with the names of A. J. Kluyver and K. L. van Schouwenburg of Delft, and to a still greater extent by E. NEWTON HARVEY (1887—), Professor of Biology at Princeton University (Fig. 883). Harvey has made the subject of bioluminescence his life-study, not only by elucidating the complicated chemistry which underlies the production of light, but also by travelling far and wide over land and sea for over forty years with all the enthusiasm of a born naturalist, observing the phenomena in the native haunts of light-producing animals. His impressive output of over 80 papers on this subject



FIG. 883.—E. NEWTON HARVEY
(1887—).

is summarized in his three classical books—*The Nature of Animal Light* (1920), *Living Light* (1940), and *Bioluminescence* (1952). Rarely has a biologist made a subject so peculiarly his own.

The Occurrence of Bioluminescence

BIO-LUMINESCENCE, the production of light by living organisms, is a very widespread phenomenon, for it is seen among fungi,¹ in many types of bacteria and in scattered representatives of all the animal phyla from Protozoa to Fishes. Several fungi² have this property, some of them parasitic on living vegetation, such as *Agaricus olearius* which grows at the foot of the olive

FIGS. 884 AND 885.—LUMINOUS ORGANS ASSOCIATED WITH THE EYES IN FISH.

In both fishes the luminous organ is a compact mass of white tissue lying underneath the eye, the back of which is covered with black pigment to keep the light from the eye of the fish. The organ is composed of a large number of glandular tubes containing luminous bacteria in great abundance which seem to be the source of the light. The organ is constantly luminous but the two fish have developed different mechanisms to extinguish the luminescence periodically (after Hein).

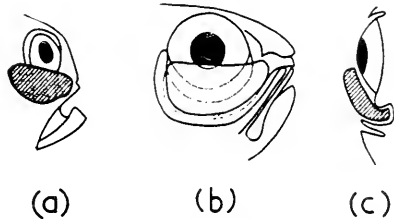


FIG. 884.



FIG. 885.

FIG. 884.—*Photoblepharon palpebratus*, showing the luminous organ (cross-hatched) exposed (a). On the ventral border of the organ is a fold of opaque black tissue which can be drawn up over the surface of the organ like an eyelid, thus extinguishing the light (b). On its retraction the luminescence again becomes evident (c).

FIG. 885.—*Anomalops katoptron*. The luminous organ (cross-hatched) is inverted into a pocket of pigmented tissue so that the light is periodically obscured.

trees of Southern Europe and served as the foundation of modern experimental work on this subject by Fabre (1855), while to others is due the luminescence of decaying wood in the forests, a phenomenon known to Aristotle. Bacteria of many types—cocci, bacilli, pseudomonas, vibrios—similarly luminesce.³ Micro-organisms are also the source of the luminescence of many molluscs and fishes, sometimes saprophytic on the surface of the animal, sometimes parasitic within it. In the squid, *Loligo*, for example, luminous bacteria are retained within open organs and in some shallow-water fishes similar symbiotic bacteria flourish in a palisade of tubules in special organs in the cheeks or lower jaw. In contradistinction to the luminescence

¹ Some green plants, mosses, for example, which live in dark caves, appear to luminesce, but the light is due to total internal reflection from spherical cells.

² For review, see Wassink (1948) who listed 65 species of luminous fungi.

³ For reviews, see Molisch (1912), Johnson (1947).

of animals which is excited only on stimulation, as a rule a bacterial or fungal glow is continuous both by night and day so long as a supply of oxygen is available; but in *Photoblepharon*, a littoral fish from the Banda Sea, the luminous organ can be covered at will with an opaque shield, while in another East Indian fish, *Anomalops*, it can be everted or withdrawn into a pouch beneath the eye where it is hidden from view so that the illusion of intermittency is given (Figs. 884 and 885) (Hein, 1913; Harvey, 1940); as these fish swim in large shoals they flash their lights at rhythmic intervals, using them probably as a social signal. Again, infection of the Amphipod, *Talitrus*, sand-fleas, squids and other organisms, with luminous bacteria



FIG. 886.—QUATREFAGES'S FAMOUS FIGURE OF *NOCTILUCA*.

Showing the irregular distribution of luminescence and the points of light coming from granules in the protoplasm (E. N. Harvey's *Bioluminescence*, Academic Press).

makes their bodies glow; while the pale luminescence of decaying fish or meat is due to harmless organisms such as *Microspira photogenica*, *Pseudomonas lucifera*, or *Micrococcus phosphoreus*. It is this which causes the pale glow of meat hanging in refrigerators or sometimes of dead bodies in the dissecting room at night; such a glow used to be a welcome sign in a pre-Listerian surgical ward for these organisms were non-suppurative.

Protozoa, however, are the most abundant source of this form of light, for to them is largely due the "phosphorescence" of the sea. Much of this is derived from the vast blankets of Radiolarians and Dinoflagellates, and particularly the dinoflagellate, *Noctiluca miliaris*,¹ which make up a large proportion of the planktonic fauna, particularly as they swarm in early summer and multiply prodigiously in the autumn. These marine organisms do not emit light unless at night and until the water in which they float is disturbed, but in the darkness a broken surface glows with sheets of cold fire and every wave-crest is aflame, while the tracks of the schools of fish become streaks of molten metal (Fig. 886). "It is impossible to behold this . . . wonderful and most beautiful appearance . . . as if [the waters]

¹ The luminescence of *Noctiluca* formed the subject of the early classical paper by Quatrefages (1850) and was extensively studied by Pratje (1921). See sketch, p. 179.

FIGS. 887 AND 888.—PANCERI'S REPRESENTATION OF A COMB-JELLY.



FIG. 887.

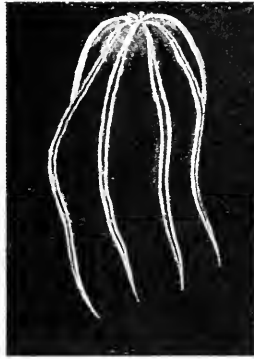


FIG. 888.

Fig. 887 by day ; Fig. 888 by night (E. N. Harvey's *Living Light*, Princeton University Press).

were melted and consumed by heat," wrote Charles Darwin of the "burning of the sea" as he sailed in the *Beagle* off the coast of Brazil. "without being reminded of Milton's description of the regions of Chaos and Anarchy."

Among the higher animals, numerous Cœlenterates show this activity—many hydroid polyps and jellyfish (particularly *Pelagia noctiluca* which forms a striking object in the Mediterranean at night) and possibly all the delicate freely-swimming Ctenophores (comb-jellies), luminescing usually over their entire surface when stimulated (Figs. 887–8). The brittle-stars (Ophiuroidea) contain the only luminescent representative of the Echinoderms. Among worms, luminescence is restricted to some species of terrestrial Oligochaetes and marine Polychaetes when they are irritated, while only one nemertean worm (*Emplectonema kandai*) has been described which luminesces when it is touched or stretched (Kanda, 1939). The marine worm, *Chætopterus*, which lies in a tube buried in the sand, forms a very striking picture indeed (compare Fig. 896).

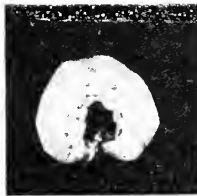
FIGS. 889 AND 890.—THE BEETLE, *PHENOGODES*

FIG. 889.

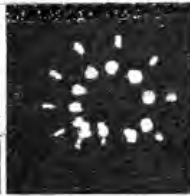


FIG. 890.

Fig. 889 the beetle by day ; Fig. 890 the beetle photographed in its own light (E. N. Harvey's *Living Light*).

The Arthropods contain many luminous species, most of them Crustaceans and Insects, a few of them Myriapods and Arachnids. Luminescence among Crustaceans is seen at its best in Copepods and Ostracods while the brilliantly luminous shrimps, *Meganctiphanes*, as they rise in immense shoals with the cold currents from the depths of the sea, glitter with millions of pin-points of light as they surface over a wide area. Several species of deep-sea Crustaceans have luminous organs, one of peculiar interest appearing anatomically as a segment of a composite compound eye (*Stylocheiron mastigophorum*—Chun, 1896).¹ Only in a few orders of Insects are luminescent types found such as the Collembola (springtails), the Hemiptera (lantern flies) and the Diptera (fungus-gnat larvæ), but the most striking examples are found among the beetles (Coleoptera) particularly the Lampyrids and Elaterids (*Lampyris noctiluca*, *Photinus pyralis*, etc.) (Figs. 889–90) ;



FIG. 891.—*LYCOTEUTHIS DIADEMA* AS IT MIGHT LOOK IN THE DEEP SEA (after Dahlgren, from a drawing by Bruce Horsfall ; E. N. Harvey's *Bioluminescence*, Academic Press).

the fascination of the signalling of the winged male fire-fly (or more correctly fire-beetle) to his wingless mate, the glow-worm, or the beauty of the rhythmic synchronous flashing of a cloud of fire-flies in a tropical evening has long attracted attention (Buck 1937–47) (Figs. 893 and 894).²

Several Molluscs are luminescent, some such as the bivalve, *Pholas*, having glandular organs in the siphon which secrete a luminous slime, while in others such as the nudibranch, *Phyllirrhoe* (the “flowing leaf” of the Mediterranean and Atlantic), they are distributed over the whole body (Trojan, 1910). The most conspicuous examples, however, are found among Cephalopods,³ about half the species of which emit light. So elaborate may the mechanism in these creatures become that up to four different colours of light are produced by the highly specialized luminous organs in certain deep-sea squids in the Pacific Ocean (the “wonder lamp” *Lycoteuthis*—Okada *et al.*, 1933 ; Takagi, 1933) (Fig. 891).

Among the Protochordates, some species of Hemichordates luminesce such as the balanoglossid, *Ptychodera* (Crozier, 1920), as well as certain colonial Tunicates such as the beautiful *Pyrosoma*: a whole colony of the latter with its numerous individuals swims as one creature and if

¹ p. 160.

² p. 58.

³ For review, see Berry (1920).

irritated exhibits a wave of photogenic activity which merits the popular name "phosphorescent fire-flame" (Polimanti, 1911). Among Fishes, there are many luminous examples, both Selachians and Teleosts, most of which inhabit the deep sea or the ocean bed; it is interesting that luminous organs are unknown among cave-fishes or fresh-water fish.¹ Some shallow-water fishes luminesce but it is in the darkness of the bathypelagic and the absolute night of the benthonic zones that bioluminescence has reached the zenith of its development. Here, far beneath the level of the plankton, the luminous organs of the molluscs and fishes are the only source of light, and Beebe (1934) has computed that two-thirds of bathypelagic species of fish including 96.5% of all individuals are luminous. Indeed, to catch these pale gleams of light would seem to be the only reason



FIG. 892.—THE HATCHET FISH, *ARGYROPELECUS*, (reproduced from Dahlgren, from a drawing by Bruce Horsfall; E. N. Harvey's *Living Light*).

for the development of the enormous eyes which characterize some of these inhabitants of the great depths.² Curiously, in bathypelagic molluscs and fishes the vast majority of these lights are directed downwards; some, differing between the two sexes, point horizontally and are obviously sexual recognition marks, but luminous organs situated dorsally are invariably minute or degenerate (Hubbs, 1938) (Figs. 892 and 895).

The *biological purpose* of bioluminescence is sometimes clear, but often obscure. It would seem that the light is never employed as a search-light whereby to see, but always as a signal-lantern as a lure, a label or a means of dazzling; for the most part they are social or sexual signals. Luminous organs of great complexity thus occur in deep-sea fishes in which the eyes are degenerate or even absent (*e.g.*, *Ipnotops*³). Their *sexual value* as an aid to courtship is the most securely proven.

Two examples will make this matter clear. The female fire-worm of Bermuda (*Odontosyllis*) at mating time seeks the surface of the sea where she circles luminescing brilliantly for 10 to 20 seconds; the male swimming in the deeper water makes for

¹ The only fresh-water luminescent animal described is an aquatic glow-worm.

² p. 322.

³ p. 724.

her ; if she stops emitting light he wanders off aimlessly but if he reaches her in time the two join together in the " mating dance," scattering sperm and eggs in a luminous spiral in the water (Galloway and Welch, 1911). The mating of the fire-fly, *Photinus*, is equally pretty. The male fire-fly dances in the air in the evening intermittently flashing a light ; in the grass the female glow-worm responds by an answering flash exactly two seconds later, turning her abdomen with its luminous organs towards him (Figs. 893-4), and immediately the male flies directly towards his mate.¹ Within a species the timing of the answering flash is the important recognition signal and the eager male can be tricked by a flash-light on the ground provided the proper interval is maintained (Buck, 1937).

Luminous flashes also serve as social signals, particularly among schools of fishes ; while a protective function is equally well established. They may

FIGS. 893 AND 894.—THE LUMINOUS ORGANS OF *LAMPYRIS SPLENDIDULA*

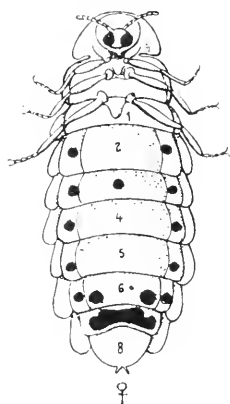


FIG. 893.—The ventral surface of the female glow-worm. There are paired lateral luminous organs on segments 2 to 6, a small median organ on segment 3, paired median organs on 6, and a large unpaired organ on segment 7.

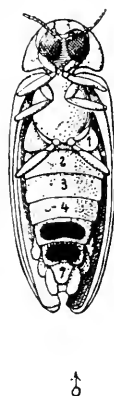


FIG. 894.—The ventral surface of the male fire-fly. There are only 2 median luminous organs on segments 5 to 6 (after Bongardt).

scare a predator or even serve as a warning to other members of the species, while they act as a means of concealment by dazzling an enemy. Thus, when attacked, the bathypelagic shrimp, *Acanthephyra*, ejects from gland-like luminous organs a luminescent cloud in which it escapes (Harvey, 1931) (Fig. 895) ; two deep-sea prawns found in the Indian Ocean emit a substance of the same nature from their antennary glands (Alcock, 1902) ; while the deep-sea squid, *Heteroteuthis*, ejects a similar cloud, the counterpart of the black ink of its shallow-water relative. A deep-sea fish, *Malucocephalus laevis*, uses a gland near the anus in the same way (Hickling, 1925-26). A peculiar sacrificial protection is suggested by the behaviour of the scale-worm, *Acholoë* ; if it is cut in two by a predator, the posterior portion

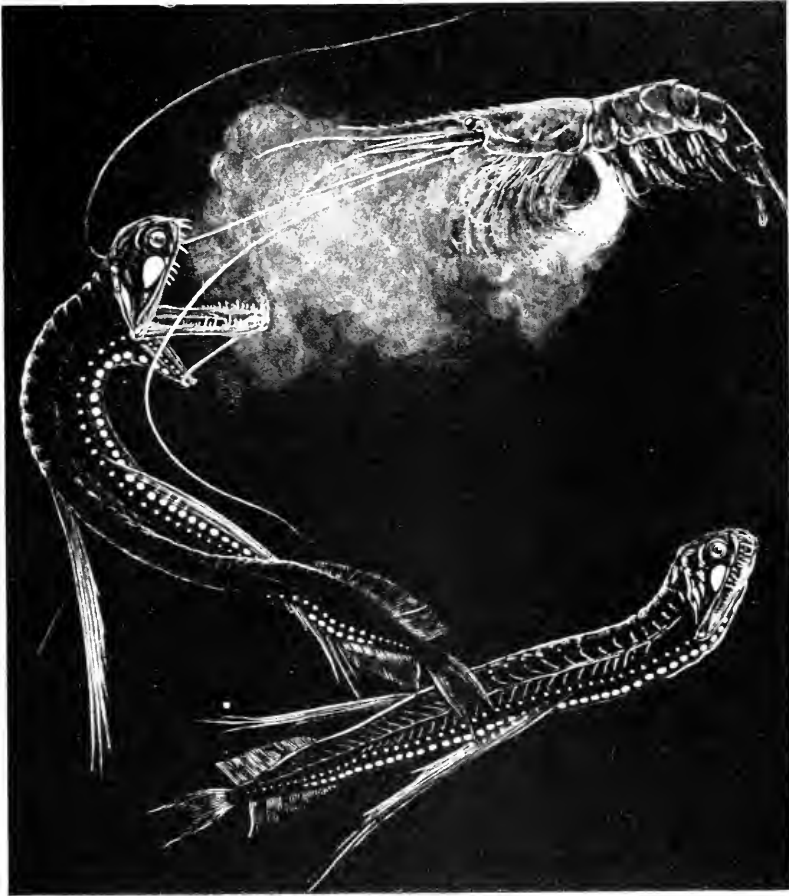


FIG. 895.—BATTLE AT SEA.

A deep-sea shrimp, *Acantheephyra purpurea*, secreting from its luminous gland to blind its foe during a battle with the fish, *Photostomias guernei*. Note the luminous organs behind the eye and on the ventro-lateral surface of the latter (reproduced by special permission from the National Geographic Society, after a painting by E. J. Geske).

luminesces brightly, presumably to attract attention. while in the vital anterior part luminescence is inhibited, perhaps in order to aid in its escape in the dark (Fig. 896).

For other functions such as the luring of prey, there is little convincing evidence, and, indeed, it would seem that in many instances, for example in the luminescence of fungi or bacteria or in many lower forms, the function can have little survival value. It may be that in those cases the light is emitted incidentally as a by-product of oxidative metabolism, a potentiality which has been seized upon for constructive purposes by certain of the higher species.

The Biological Mechanism of Bioluminescence

We have already noted the exploitation of the adventitious light produced by luminous bacteria which occurs in certain molluscs, crustaceans and fishes ; these may be either symbiotic or parasitic in habit.¹ Apart



FIG. 896.—SCALE-WORM ATTACKED BY A CRAB.

The rear half, used as a sacrificial lure, is brightly luminescent to attract the attention of the crab, while the front portion ceases to luminesce and crawls away in the shadow to reproduce a new tail (reproduced from Dahlgren, from a drawing by Bruce Horsfall ; E. N. Harvey's *Living Light*).

from these, animals produce bioluminescence in one of two ways—either extracellularly or intracellularly. In unicellular organisms light-producing granules are scattered throughout the cytoplasm, particularly near the periphery, and on stimulation a glow passes like a wave throughout the cell (Quatrefages, 1850 ; Pratje, 1921). In multicellular animals,

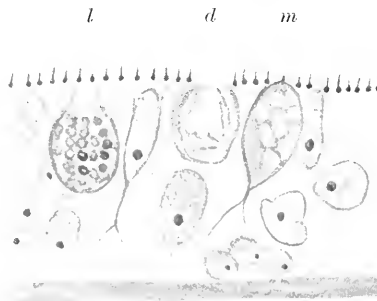


FIG. 897.—SECTION OF THE ABORAL UMBRELLA SURFACE OF *PELAGIA NOCTILUCA*.

Showing luminous cells, *l*, mucous cells, *m*, and cells with contents discharged, *d* (modified from Dahlgren)

¹ p. 737.

however, special luminous organs are evolved for the production of the photogenic materials.

In *extracellular bioluminescence*, gland-like organs on the surface of the body secrete a photogenic material which becomes luminous on contact with the oxygen of the air or the sea-water. Such glands may be unicellular or multicellular. This mechanism accounts for the luminescence of Coelenterates; in the jellyfish, *Pelagia noctiluca*, for example, single gland-like cells lie in the epidermis and stimulation, as by touching the animal, during the evening but not during the daylight hours, produces the secretion of a luminous mucus which spreads like a wave over it and can be rubbed away

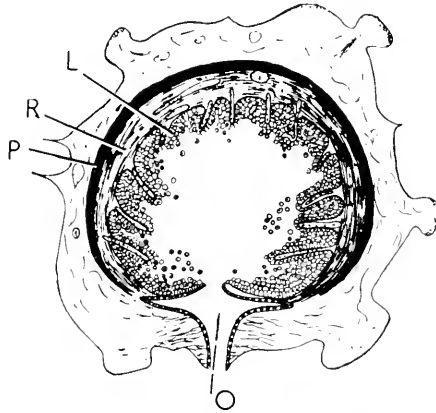


FIG. 898.—SECTION OF THE LIGHT ORGAN IN THE ESCA OF THE ANGLER-FISH, *GIGANTACTIS*.

Showing luminous epithelium, L; reflector layer, R; pigment layer, P; and the opening of the lumen into a second cavity which communicates with the outside, O (after Brauer; E. N. Harvey's *Bioluminescence*, Academic Press).

with the finger (Dahlgren, 1915–17; Parker, 1920; Harvey, 1921; Moore, 1926) (Fig. 897). Such a spread indicates transmission of the stimulus by a nerve-net; the process is inhibited in the absence of Ca or K, and irritability is markedly increased in the absence of Mg (Heymans and Moore, 1924). A somewhat similar luminous slime is produced by many worms; in the luminous earthworm it emerges from the mouth or anus or from dorsal pores (Gates, 1925; Komarek, 1934), and in Polychaetes the photogenic cells are situated in association with mucous cells in the hypodermis (*Chaetopterus*—Dahlgren, 1916) or in specific locations (e.g., in specialized nephridial funnels in the transparent marine worm, *Tomopteris*—Meyer, 1929). Again, a wave of light-production from the point of excitation indicates a spread by nervous means. A similar slime is secreted by the clam, *Pholas*, luminous Myriapods, and the colonial ascidian, *Pyrosoma*. Glandular organs of a more complex type are seen in Crustaceans in which granules are secreted

and when ejected into the sea-water, appear as a luminous cloud (Fig. 895). In Copepods the photogenic cells are in small groups; in the Ostracod, *Cypridina*, there is a complex gland of 4 types of cell near the mouth from which granules are ejected by muscular action (Okada, 1926 ; Takagi, 1936) ; a similar mechanism is found in the deep-sea shrimps and squids (Harvey, 1931). In these the operative mechanism is neuro-muscular. Finally, in some bathypelagic fishes such as *Malacocephalus* or *Gigantactis*, similar luminescent granules (which may be bacterial) are expelled on the ventral surface of the body from sac-like organs when the fish is excited (Fig. 898).

The intracellular production of bioluminescence is more widespread, and, again, may be effected either by single cells or elaborate organs equipped with secretory cells, a lens and cornea, light-absorbing and light-reflecting structures, the whole resembling in many ways a well-formed eye. Such organs are called PHOTOPHORES. The luminous brittle-stars and the nemertean worm, *Emplectonema*, have single light-producing cells scattered over their entire surface (Kanda, 1939). The Arthropods, however, show more specialized photophores as are seen particularly in shrimps, consisting of large granular light-producing cells lying underneath an epithelial lens and upon a reflecting layer (Fig. 899) (Vallentin and Cunningham, 1888 ; Terao, 1917). Organs of a somewhat similar type, consisting of photogenic cells, a lens and a reflector

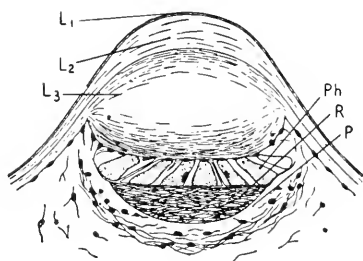


FIG. 899.—SECTION OF A PHOTOPHORE OF THE DECAPOD SHRIMP, *SERGESTES PREHENSILIS*.

Showing the lens layers, L_1 to L_3 ; photogenic cells, Ph ; reflector, R ; and pigment, P (after Terao ; E. N. Harvey's *Bioluminescence*, Academic Press).

surrounded by pigment, frequently occur in Molluscs, and also in many deep-sea Fishes arranged along the ventro-lateral aspect of the body. The photophores of Insects are equally elaborate. In the fire-fly, *Lampyrus*, for example, the luminous organ is situated ventrally in the posterior part of the abdomen ; it consists of a layer of light-producing cells lying under the surface epithelium, backed by a layer of light-reflecting cells which owe their optical property to small particles of urates, while an abundance of oxygen is provided by a rich supply of tracheæ (air tubes) equipped with end-cells which act as minute pumps or valves (Fig. 900) (Hess, 1922). All these photophores are well supplied with nerves and appear to be under nervous control except in some fishes ; studying the luminous organs of the Californian stinging fish, *Porichthys*, Greene and Greene (1924) failed to find any nerves and demonstrated that they were under hormonal control, the whole animal remaining alight and glowing for over an hour after a subcutaneous injection of adrenalin. It is noteworthy,

as we have already seen,¹ that a central nervous control is made manifest in many species by the presence of a diurnal rhythm, whereby the 24-hour phase of luminescence persists even if the animal is kept in continuous darkness for some time (the jellyfish, *Pelagia*—Heymans and Moore, 1924 ; the fire-fly, *Photinus*—Buck, 1937 ; the balanoglossid, *Ptychodera*—Crozier, 1920).

The Chemical Mechanism of Bioluminescence

Despite the expenditure of much study and speculation since the time of Aristotle, the intimate chemical nature of bioluminescence is not yet

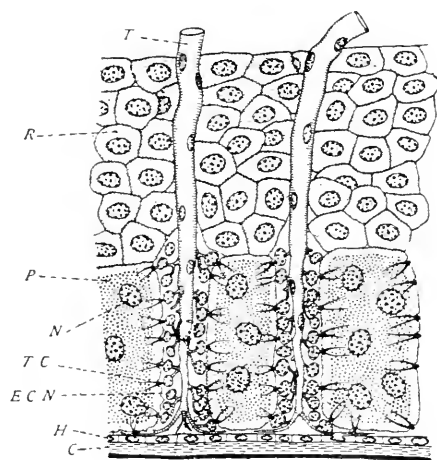


FIG. 900.—CROSS-SECTION OF THE LIGHT ORGAN OF AN INSECT.

The light organ of the adult *Photurus pennsylvanica*. C, cuticle ; ECN, nucleus of tracheal end-cell ; H, hypodermis ; N, nucleus of photogenic cell ; P, photogenic layer ; R, reflector layer ; T, trachea ; TC, tracheole (W. N. Hess, *J. Morphol.*).

clear. The process is the reverse of a photochemical reaction wherein the absorption of light induces chemical activity ; here the energy derived from a chemical reaction is converted into light. Such a chemical reaction is oxidative in nature and converts a substance into an activated state in which it can emit light as it lapses again into the non-activated state. The occurrence of chemiluminescence in the inanimate world has long been known ; it is shown, for example, by phosphorus² and a multitude of organic

¹ p. 21.

² PHOSPHORESCENCE, properly defined, is a delayed fluorescence. FLUORESCENCE occurs when a substance, on radiation, emits light of a wave-length differing from the incident light. The incident light is absorbed by molecules which are thereby changed into an activated form ; these return to their original state giving off energy as they do so ; this energy, being absorbed by other molecules capable of radiation, is emitted as *fluorescent light*. By delaying the energy transfer, the emission of light occurs sometime after exposure as PHOSPHORESCENCE. The commercial sulphides of Ca, Ba and Sr possess the property of phosphorescence and are used in luminous paints.

compounds in solution. That bioluminescence is also a simple chemical reaction not associated with the metabolic integrity of living cells has also been appreciated for a long time, for on desiccation of the cells or their products, luminescence ceases but recommences on the addition of water in the presence of oxygen. The role of the cells is to produce and store the reacting substances and bring them together at the appropriate time. Luminous cells are always granular and their production of light is associated with the dissolution of the granules, either on their extrusion into sea-water or on the complete breakdown of the organization of the cell in the act of secretion (Hickling, 1925-26).

For luminescence to occur, water is always necessary, and in most cases oxygen either in the air or dissolved in water, a fact first discovered by the great English natural philosopher, Robert Boyle (1667).¹ Sometimes, as in the case of certain radiolarian Protozoa and some Cœlenterates such as the jellyfish, *Pelagia*, and the comb-jelly, *Mnemiopsis*, luminescence occurs in the absence of free oxygen: the fact that Harvey and Korr (1938) found that the extract of the last organism became luminous in the presence of nascent hydrogen suggests that in such cases bound O₂ is made available by the appropriate stimulus.

It was first shown by Dubois (1885-87), studying the luminescence of the beetle, *Pyrophorus*, and the clam, *Pholas*, that the reaction involved two substances, the one, LUCIFERASE, a heat-labile, non-dialysable, protein-like substance with the characteristics of an enzyme, the other, LUCIFERIN, a readily oxidizable, diffusible substance of low molecular weight and undetermined chemical composition.² These two substances have been identified in some polychæte worms, crustaceans and beetles, and although they are apparently absent in most luminous species, it has been assumed that a system resembling luciferase-luciferin is the basis of most reactions. Luciferin is readily oxidized in many ways but luminescence appears only when the reaction is catalyzed by luciferase. It used to be generally accepted that in the reaction the light was emitted by molecules of activated luciferase (Harvey, 1917), but further study has shown that the matter is probably not so simple. Glucose and phosphates appear to be important in the reaction, suggesting a relation with the carbohydrate metabolism (McElroy and Ballentine, 1944), but the intimate nature of the process, whether the emitting molecule is luciferase or luciferin or even another unidentified substance, or how far the reactions occurring in different species are alike, are all matters which must await further research (see Chance *et al.*, 1940; Chase, 1940; Harvey, 1940; Khuyver *et al.*, 1942;

¹ *New Experiments Physico-mechanical touching the Spring of Air and its Effects*, London, 1660-82.

² Anderson (1933-36), who first purified luciferin, considered it a polyhydroxy benzene derivative; Chakravorty and Ballentine (1941) identified a ketohydroxy side-chain and a hydroquinone ring; and Eymers and van Schouwenburg (1936) suggested a derivation from flavine. Using chromatography, however, McElroy and Strehler (1949) found that the compound generally described as luciferin had at least three constituents—a bivalent metallic ion (Mg, Mn, Co), adenosine triphosphate, and a further unidentified compound.

McElroy and his co-workers, 1944-51 ; Johnson *et al.*, 1945 ; and others). Nor is it known how the reaction *in vivo* is inhibited by light, particularly short-waved light, whether by a destruction of the photogenic precursors or an inhibition through the controlling nervous (or hormonal) mechanism (Harvey, 1925 ; Heymans and Moore, 1925).

The nature of the light involved in bioluminescence varies with different species and even in the same animal. In intensity it is relatively low ; in the fire-fly, *Photinus*, for example, it is the equivalent of from 0.0025 to 0.02 candles (Coblentz, 1912). In colour it varies from blue to red, usually extending over a considerable range and showing a continuous spectrum ; but ultra-violet is never present and it is " cold " in the sense that infra-red is also absent (Harvey, 1920 ; Buck, 1941).

The large bibliography, particularly of the biochemical problems involved, will be found in E. N. Harvey (1920, 1940, 1952), F. A. Brown in Prosser's *Comparative Animal Physiology*, London, p. 660 (1950), and H. Davson's *Textbook of General Physiology*, London, p. 600 (1951).

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CHAPTER XXII

ELECTRIC ORGANS

A GREAT many fishes are possessed of an electric organ—a curious specialization found only in this class of Vertebrates. They are all developed from modified muscular tissue formed into plates arranged in series ; the only exception is that of the electric catfish, *Malopterurus*, which is developed from cutaneous glands (Garten, 1910). When a muscle contracts the energy

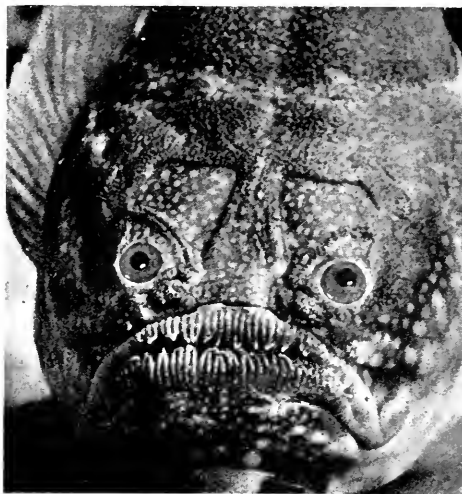


FIG. 901.—THE STARGAZER, *ASTROSCOPUS*.

The electric organs are seen as the flat areas behind the eyes. The fish normally lies buried in the mud with only the eyes, mouth, electric plates and a fin showing, so that the small fish which swim too near are electrocuted and fall straight into the ugly open mouth (Alice Jane Mansueti, Chesapeake Biol. Lab., Maryland, U.S.A. : from the *Illust. Lond. News*).

developed is expended in motion, heat, and electricity ; in electric organs the electrical properties, in place of being subsidiary, become predominant. Among Selachians, in electric rays (*Hypnarce*, *Torpedo*) the organ is immense, running through the entire thickness of the body between the head and the pectoral fin ; in other rays and in the teleostean electric eel, *Electrophorus*, it is smaller and situated at the sides of the root of the tail. In the American stargazer, *Astroscopus*, however, the great rarity is found of an electric organ situated in the orbit derived from the extra-ocular muscles, all of which with the exception of the inferior rectus and the inferior oblique, while retaining to some extent their original function, have become modified

for this purpose (White, 1918 ; Woelfflin, 1955) (Fig. 901). The electric organ of the stargazer assumes a considerable size, about 1/10 of the length of the body, and occupies most of the space of the enlarged orbit so that the small eye, protected by an unusually thick sclera, is crowded into its anterior

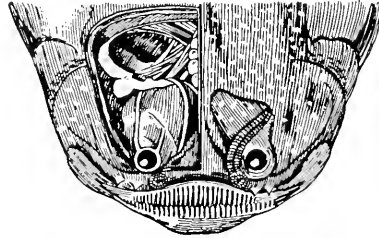


FIG. 902.—THE ORBIT OF THE STARGAZER.
Showing the electric organ (Bland-Sutton).

portion (Fig. 902) ; although the organ is relatively large, the shock derived from it, while somewhat unpleasant, is a mere tickle compared with that of certain electric fishes which can knock a man off his feet. The upward-looking eyes are situated on the upper aspect of the head just in front of the mouth, and as small fishes swim over the stargazer, it paralyses them with an electric shock so that they tumble into its gaping mouth (Dahlgren and Sylvester, 1906).

Dahlgren and Sylvester. *Anat. Anz.*, **29**, 387
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3, 105 (1910).

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EPILOGUE

This is the story of the development of the eye from the primitive undifferentiated protoplasm of the simplest protozoon to become the most highly efficient sensory mechanism in the animal kingdom in the eyes of Birds. It is the story of the development of the sense of vision from an automatic response, associated at some stage with a vague awareness, to the capacity to be enraptured by a sunset or a rainbow or to create a thing of beauty. The first story is factual; the second speculative.

The subject of the second is fraught with difficulties so great as to make a final solution impossible. In the physical world material things are incomprehensible to each other and can be analysed only on a higher level by the senses; the sense-organs know nothing of each other for sensations can be analysed only by perceptions; we have no access to a platform wherefrom to look down upon perceptions and subject them to analysis. It follows that our consciousness is to us unknowable and will probably remain so—until or unless we acquire other and higher faculties. And if we, in our wordy thinking, cannot mutually compare the symbolic representation that each of us creates perceptually of the outside world, how much more difficult to analyse what the animal world in its wordless thinking makes of it.

A hypothesis might run like this. There are three stages in the evolution of vision. It started as a motor taxis, appearing initially in the simplest unicellular organisms as an automatic response which eventually became more plastic to reach its culmination in the homing bird; as such it need not enter consciousness. From this emerged perceptual vision, a pragmatic sense, essentially a passive registration of objects in the outside world, serving primarily the biological needs of hunger, fear or sex. Initially a minor, it eventually became a major determinant of conduct. Dependent on a central nervous organization to create its symbolism, it started in worms and reached its highest level in man. From this emerged imaginative vision with its aesthetic and creative qualities, with its inquisitive, exploratory drive, seeing beauty. It depended on the almost explosive development of the frontal brain in the highest Primates. It first appeared, presumably, during the ape-man's arboreal adventure and certainly is present in the chimpanzee; it was well established when modern man migrated northwards following the melting of the ice 20,000 years ago to replace his Neanderthal predecessors and establish the Aurignacian and Magdalenian cave-civilizations in south-west Europe, and reaches its greatest development, perhaps, in the human mind relieved of the chemical servitude of inhibitions, as by mescaline.

It is a fascinating story extending back to where life started, a story mostly of steady progress, now in this direction, now in that, as one expedient after another was tried, this one to be discarded, that to be perfected. It is a long story, and in this Volume it can only be sketchily told.

In the volumes of this series which follow we will discuss in more detail the visual apparatus of man—its structure, its development, its function, and the effects upon it of disease and injury.

APPENDIX

ERAS	PERIODS AND SYSTEMS	DATES IN MILLIONS OF YEARS (Approx.) at beginning of period
CENOZOIC (καινός = recent ; ζωή = life)	QUATERNARY	HOLOCENE (ὅλος = complete ; καινός = recent)
		PLEISTOCENE 1 (πλεῖστος = most)
	TERTIARY	PLIOCENE 12 (πλείων = more)
		MIOCENE 29 (μείων = less)
		OLIGOCENE 40 (ὀλίγος = few)
		EOCENE 60 (ἥως = dawn)
		PALÆOCENE 75 (παλαιός = ancient)
MESOZOIC (μέσος = middle)		CRETACEOUS 135 (Creta = chalk)
		JURASSIC 175 (Jura mountains)
		TRIASSIC 210 (Threefold division in Germany)
PALÆOZOIC (παλαιός = ancient)	Upper	PERMIAN 240 (Permia = ancient kingdom E. of Volga)
		CARBONIFEROUS 290 (Coal-bearing)
		DEVONIAN 320 (Devon's marine rocks)
	Lower	SILURIAN 350 (Silures = ancient tribe of Welsh borders)
		ORDOVICIAN 420 (Ordovices = ancient tribe of N. Wales)
		CAMBRIAN 500 (Cambria = Wales)
PRE-CAMBRIAN ERAS		PROTEROZOIC ? (πρότερος = earlier)
		ARCHÆOZOIC ? (ἀρχαῖος = primæval)

PALÆONTOLOGICAL TABLE

Australopithecus ; Pithecanthropus ; Homo

Eutherian mammals become numerous and diverse. Grasses appear in Miocene. Brachiopods diminish in importance ; lamellibranchs abundant. Insects associated with flowering plants radiate now.

First appearance of : urodeles, snakes, marsupials, insectivores, modern-type flowering plants. At end of period extinction of saurischian and ornithischian dinosaurs, pterosaurs, plesiosaurs, ichthyosaurs, ammonites.

First appearance of : plesiosaurs, ornithischian dinosaurs, pterosaurs, birds, anurans, flowering plants. Radiation of cartilaginous and actinopterygian fishes.

First appearance of : saurischian dinosaurs, ichthyosaurs, chelonians, crocodiles, rhynchocephalians, lizards, and, at end of period, mammals. First moss. Hexacorals and lamellibranchs rise to prominence in marine faunas. By end of period extinction of " labyrinthodonts " and cotylosaurs.

First appearance of : true ammonites, holostean fish. Trilobites and rugose corals extinct at end of period, also acanthodians. Endopterygote insects appear at beginning of period.

First appearance of : reptiles and conifers (upper Carb.). All arachnid groups have now appeared except possibly mites. Foraminifera become abundant.

First appearance of : placoderms, rhipidistia, dipnoi, sharks, actinopterygians, insects, myriapods, and at end of period, coelacanth and amphibia. Placoderms except acanthodians, become extinct at end of period, as do the bony ostracoderms.

First appearance of : ammonoids, scorpions and, at end of period, land-plants, 4 groups agnathan fish, acanthodians. Graptoloids become extinct at end of period.

First appearance of : corals, echinoderms (blastoids, crinoids, starfish, echinoids), lamellibranchs, ectoprocts (polyzoa), ostracods, graptolites, ostracoderms (fragmentary), eurypterids.

First appearance of : sponges (siliceous), coelenterates (medusæ), echinoderms (cystids and some which are probably Holothurian), annelids, brachiopods (small " horny " hingeless), molluscs (gastropods, pteropods, nautiloids), arthropods (onychophora, trilobites, crustacea), graptolites. Algæ present.

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ZOOLOGICAL GLOSSARY

The figures in bold face indicate the number of a page containing an illustration in the text; those in italics indicate the number of a page showing a marginal illustration.

- ABLEPHARUS*. Skink: a reptile of the lizard family.
- ACANTHEPHYRA*. Deep-sea shrimp: decapod crustacean.
- ACARINA*. An order of Arachnida, many of them minute and parasitic (mites, ticks).
- ACCIPITER*. Sparrow-hawk: bird-of-prey (Falconiformes).
- ACEKENTOMON*. Wingless, eyeless insect: Protura, 218.
- ACHIAS ROTHSCHILDI*. Stalk-eyed fly: dipterous insect, 223.
- ACHOLOË*. Scale-worm: free-swimming polychæte worm.
- ACHIUS*. Water-beetle: coleopterous insect.
- ACIPENSER*. Sturgeon, sterlet: chondrosteian fish, 317.
- ACNIDARIA*. Sub-phylum of non-stinging cœlenterates, comprising the ctenophora.
- ACRIDA*. Short-horn grasshopper: an orthopterous insect (Acrididæ).
- ACROBATES*. Flying phalanger: marsupial.
- ACTINIA*. Sea-anemone: cœlenterate (Anthozoa).
- AËDES*. Mosquito: dipterous insect.
- ÆGA*. A crustacean (Isopoda).
- ÆGLINA PRISCA*. Trilobite: extinct arthropod, 157
- ÆSCHNA*. Dragonfly: insect (Odonata), 222, 225
- AGAMA AGAMA*. Agamid lizard: a lacertilian reptile, 359
- AGARICUS OLEARIUS*. Luminous fungus.
- AGNATHA*. Class of jawless pre-fishes: the earliest vertebrates, represented today only by the Cyclostomata.
- AHEYLLA PICTA*. Painted tree snake: a colubrid snake.
- AILUROPODA MELANOLEUCA*. Giant panda: carnivore (Procyonidæ).
- AILURUS FULGENS*. Panda: carnivore (Procyonidæ).
- ALAURINA PROLIFERA*. Pelagic Rhabdocœle: turbellarian worm.
- ALBURNUS*. Teleostean fish (Cyprinidæ).
- A. LUCIDUS*. The bleak.
- ALCEDO*. Kingfisher: Coraciiformes, 417
- ALCIDÆ*. The auk family of birds.
- ALCIOPA*. Free-swimming polychæte worm.
- ALLIGATOR*. Reptile, crocodilian.
- ALLOLOBOPHORA*. Oligochæte worm.
- ALOUATA*. Howling monkey: Primate (Cebidæ).
- ALYTES OBSETRICANS*. Obstetric toad: anuran amphibian.
- AMBLYOMA POMPOSUM*. Tick: Acarina (Ixodides), 217
- AMBYLOPSIS*. American cave-fish: teleostean fish.
- AMBLYRHYNCHUS CRISTATUS*. Marine iguanid lizard of Galapagos Islands: Reptile.
- AMBYSTOMA TIGRINUM*. N. American terrestrial salamander: urodelan amphibian, 346.
- AMEIURUS*. Bullhead cat-fish: siluroid teleost, 307
- AMIA CALVA*. Bowfin of N. America: holostean fish, 321
- AMMOCETES*. Larva of lamprey: cyclostome, 92
- AMMOMAXEN*. Desert lark: passerine bird.
- AMMOPHILA*. Digger wasp: insect (Hymenoptera).
- AMËBA PROTEUS*. Protozoon (Rhizopod), 179
- AMPHIOXUS (BRANCHIOSTOMA)*. Lancelet: a protochordate (Cephalochordate), 229.
- AMPHIPORUS*. Nemertine worm, 189
- AMPHIBENA PUNCTATA*. Legless blind subterranean lizard: Reptile.
- AMPHITRETUS*. Pelagic octopus: cephalopod mollusc, 203
- AMPHIUMA*. "Congo snake" or blind-eel, a salamander: urodelan amphibian, 349

- ANABAS SCANDENS*. Climbing perch: an amphibious teleostean fish.
- ANABLEPS TETROPTHALMUS*. "Four-eyed" fish: a cyprinodont teleostean fish, **325**
- ANATIDÆ. Family of birds, comprising swans, geese, ducks.
- ANAX*. Dragonfly: insect (Odonata).
- ANCALA FASCIATA*. Gadfly: dipterous insect (Tabanidæ).
- ANGUILLA*. Common genus of eel: teleostean fish, **46**
- ANGUIS FRAGILIS*. Slow-worm: legless lizard, reptile, **363**
- ANIELLA*. Worm-lizard: Reptile.
- ANNELIDA. The phylum of segmented worms, comprising Oligochaetes, Polychaetes, Leeches.
- ANODONTA*. Eyeless swan-mussel: fresh-water bivalve mollusc, **201**
- ANOLIS*. American "chameleon": iguanid lizard: Reptile, **361**
- ANOMALOPS KATOPTRON*. Luminous fish: teleost (sea-bass family).
- ANOPHELES*. Malaria-carrying mosquito: dipterous insect.
- ANOPHTHALMUS*. Blind cavernicolous beetle: coleopterous insect.
- ANOPLURA. Order of insects (wingless lice, parasitic on mammals).
- ANOPTICHTHYS JORDANI*. Blind Mexican cave-fish: teleost.
- ANSER*. Goose: Anseriformes (Anatidæ).
- ANSERIFORMES. Order of birds, comprising (mainly) the Anatidæ.
- ANTHOLOBA*. Sea-anemone: cœlenterate (Anthozoa).
- ANTHOZOA. Class of cœlenterates comprising sea-anemones and corals ("flower animals").
- ANTHROBIA*. Eyeless cave-spider: arachnid (Araneida).
- ANTHROPOIDEA. Sub-order of Primates, comprising monkeys, apes and man.
- ANTILOCAPRA*. Pronghorn: a ruminant similar to antelope.
- ANURA. Order of tail-less amphibians (frogs, toads).
- APHANIPTERA. An order of insects comprising the wingless, blood-sucking fleas.
- APHIS FORBESI*. Strawberry root louse: hemipterous insect.
- APHROPHORA SPUMARIA*. Frog-hopper or spittle-insect: hemipterous insect.
- APHYONUS*. Blind deep-sea teleostean fish.
- APIS*. Honey-bee: hymenopterous insect, **58**
- APLOCHEILICHTHYS RUBROSTIGMA*. Killifish: cyprinodont teleostean fish.
- APODA. Cecilians: an order of worm-like, subterranean amphibians.
- APODEMUS*. Field-mouse: a rodent (Muridæ).
- APTERYX*. Kiwi: flightless New Zealand bird (Ratitæ), **398**
- APUS (TRIOPS)*. Fresh-water crustacean (Branchiopod), **208**
- ARACHNIDA. Class of arthropods, comprising spiders, scorpions, king-crabs, etc.
- ARANEIDA. Order of Arachnida, comprising spiders.
- ARANEUS DIADEMATUS*. Common garden spider: arachnid (Araneida), **214**
- ARCA*. Noah's ark shell: bivalve mollusc.
- ARCHANNELIDA. Class of marine segmented worms (e.g., *Dinophilus*).
- ARCHISTOMA BESSELI*. Springtail: primitive wingless insect (Collembola).
- ARCTOCEBUS*. Agwantibo: nocturnal lemuroid (Primate).
- ARDEA*. Heron (Ciconiiformes), **494**.
- ARENICOLA MARINA*. Lob-worm: burrowing polychæte worm, **190**
- ARGYROPELECUS*. Hatchet fish: deep-sea luminous teleostean fish, **322**
- ARIOLIMAX*. Slug: gastropod mollusc (Pulmonate).
- ARISTELLIGER*. Gecko: reptile of the lizard family.
- ARISTEOMORPHA*. Shrimp: decapod crustacean.
- ARMADILLIDIUM*. Pill-bug, a terrestrial woodlouse: crustacean (Isopoda), **45**
- ARTEMIA*. Brine-shrimp: crustacean (Branchiopod), **207**
- ARTHROPODA. Phylum of invertebrates, comprising Onychophora, Crustacea, Myriapoda, Arachnida, Insecta.
- ARTIODACTYLA. Order of placentals, comprising pig, camel, deer, etc.
- ASCARIS*. Parasitic round worm: nematode, **190**
- ASCIDIA*. Sea-squirt: protochordate (Tunicate), **228**
- ASELLUS*. Blind fresh-water louse: crustacean (Isopoda), **207**
- ASIO*. Long-eared owl: Strigidæ.
- ASPLANCHNA*. A genus of rotifer.
- ASTACUS*. Crayfish: decapod crustacean, **164**

- ASTERIAS*. Starfish: an echinoderm (Asteroidea), **185**
ASTEROIDEA. Class of Echinodermata, comprising starfishes.
ASTROSCOPUS. Stargazer: teleostean fish, **751**
ASTUR PALUMBARIUS. Goshawk: bird-of-prey (Falconiformes), **403**
ATELES. Spider monkey of S. America: Primate (Cebidæ), **689**
ATHERINA. Silverside: teleostean fish, **617**
ACURELIA. Common jellyfish: a cœlenterate (Scyphozoa), **183**
AUSTROLETHOPS. Goby fish: teleostean fish.
AVICULA. Pearl oyster: bivalve mollusc, **200**
- BALÆNA*. Right-whale: a cetacean.
BALÆNOPTERA. Blue whale: the largest cetacean, **444**.
BALANOGLOSSUS. Acorn worm: a protochordate (Hemichordate), **227**
BALANUS. Acorn-shell: a crustacean (Cirripede), **209**
BALISTES. File-fish (trigger-fish): a teleostean fish.
BARATHRONUS. A deep-sea teleostean fish.
BARBATULA. A fresh-water teleostean fish.
BATHOTHAUMA. Deep-sea squid: a cephalopod mollusc, **203**
BATHYGOBIUS. Goby fish: a teleostean fish.
BATHYLAGUS BENEDICTI. Deep-sea salmonid: a teleostean fish, **310**
BATHYPTERIS. Feeler-fish: a deep-sea teleostean fish.
BATHYTEUTHIS. Deep-sea octopod: a cephalopod mollusc.
BATHYTROCTES. A deep-sea teleostean fish.
BATOIDEI. Sub-order of flat selachians (skate, ray).
BDELLOSTOMA. Slime hag: a cyclostome.
BELIDEUS SCIUREUS. A squirrel-like phalanger: marsupial (Phalangeridæ).
BELONE. Needle-fish (garfish): a teleostean fish.
BENGALICHTHYS. Deep-sea ray: a batoid selachian fish.
BENTHOBATIS. Deep-sea ray: a batoid selachian fish.
BERYX. A deep-sea teleostean fish, **303**
BETTA PUGNAX or *SPLENDENS*. Siamese fighting fish: a fresh-water teleostean fish, **84**
BIBIO MARCI. April fly: a dipterous insect.
BITIS ARIETANS. African puff adder: a snake of the viper family, **392**
BIVALVES (Lamellibranchis). Class of molluscs, comprising the shell-fish (clam, cockle, mussel).
BLATTELLA GERMANICA. German cockroach: insect (Orthoptera).
BLATTA ORIENTALIS. Common cockroach, black beetle: insect (Orthoptera), **34**
BLENNIUS. Blenny: a teleostean fish, **310**
BOIDÆ. Family of snakes, comprising boas, pythons, etc.
BOIGA DENDROPHILA. Black-and-gold tree-snake (Mangrove snake): Opisthoglyph.
BOLITOTHERUS CORNUTUS. A species of beetle: insect (Coleoptera).
BOMBINATOR (*BOMBINA*) *IGNEUS*. Fire-bellied toad: an anuran, **339**
BOMBUS. Bumble-bee: a hymenopterous insect, **219**
BOMBYLIUS. Bee-fly: a dipterous insect, **219**
BOMBYX. Silk-moth: a lepidopterous insect.
BORODINCLA INFANS. Snipe-eel: a deep-sea teleostean fish, **679**
BOS TAURUS. European domestic cattle (ox, cow): Ruminants (Bovidæ).
BOTAURUS. Bittern: a bird of the heron family, **685**
BOUGAINVILLEA. Hydroid colony: a cœlenterate (Hydrozoa).
BOVIDÆ. Family of ungulates, comprising ox, sheep, goat, etc.
BOX. Sea-bream: a teleostean fish.
BRACHIOPODA. Lamp-shells: a phylum of Invertebrata.
BRADYPUS TRIDACTYLUS. Three-toed sloth: Xenarthra (Bradypodidæ).
BRANCHELLION. Leech: an annelid (Hirudinea), **193**
BRANCHIOMMA VESICULOSUM. A marine tubicolous polychæte worm, **192**
BRANCHIONUS. A genus of rotifer.
BRANCHIOPODA. An order of crustaceans, comprising Phyllopoda and Cladocera.
BUBO. Eagle-owl: Strigidæ, **422, 606**
B. ASCALAPHUS. Savigny's eagle owl.

- BUBO LACTEUS*. Milky eagle-owl.
B. ORIENTALIS. Oriental eagle-owl.
BUCCINUM. Common whelk (buckie): gastropod mollusc, **197**
BUFO. Common genus of toad: an anuran amphibian (Bufonidæ), **341**
B. ARENARUM. S. American toad.
B. BUFO. Common toad.
B. MARINUS. Giant toad.
B. VIRIDIS. Green toad.
BUGULA. Sea-mat; colonial Polyzoon, **46**
BUTEO BUTEO. Buzzard: a bird-of-prey (Falconiformes), **417**
- CABRITA*. Indian lizard: Reptile.
CACATUA ROSEOCAPPELLA. Australian cockatoo : Psittaciformes.
CACICUS CELA. Yellow hang-nest: passerine bird (oriole family).
CÆCILLIA. A cæcilian: worm-like amphibian (Apoda).
CAIMAN. A crocodilian reptile similar to the alligator, **375**
CALAMOICHTHYS. A chondrosteian fish, **320**
CALANUS. Salt-water copepod crustacean.
CALIGUS. Fish-louse: a parasitic copepod crustacean.
CALLIACTIS. Sea-anemone: a cœlenterate (Anthozoa).
CALLIONYMUS. Dragonet: a teleostean fish.
CALLIPHORA. Bluebottle (blow-fly): a dipterous insect, **219**
CALOTERMES. Termite: an insect (Isoptera).
CALYPTÉ. Humming-bird: Coraciiformes.
CAMBARUS. Crayfish: a decapod crustacean.
CAMELUS BACTRIANUS. Camel: an artiodactyl (Tylopoda).
C. DROMEDARIUS. Dromedary.
CANIS AUREUS. Jackal: a carnivore (dog family).
C. FAMILIARIS. Dog.
C. LUPUS. Wolf.
CAPRA. Goat: a ruminant (Bovidæ).
CAPRELLA. "Skeleton shrimp": an amphipod crustacean, **207**
CAPRIMULGUS EUROPEUS. Goat-sucker (night-jar): Coraciiformes, **410**
CARASSIUS AURATUS. Goldfish: a cyprinoid teleostean fish, **292**
CARUSIUS. Leaf-insect: orthopterous insect (Phasmid).
CARCHARODON. White-tip shark: a selachian fish.
CARCINUS. Common genus of crab: a decapod crustacean.
CARDIUM. Cockle: a bivalve mollusc, **200**
CARINARIA. Pelagic heteropod: a gastropod mollusc, **199**
CARINATÆ. Sub-class of birds, comprising all the flying birds.
CARNIVORA. An order of flesh-eating mammals comprising the Fissipedia and Pinnipedia.
CASTOR. Beaver: an amphibious sciuriform rodent, **442**.
CASCARIUS. Cassowary: flightless bird (Ratitæ), **406**.
CATARRHINES. Old World monkeys (Cercopithecidæ and anthropoid apes).
CAUSUS RHOMBÆATUS. Cape viper: viperid snake.
CAVIA PORCELLUS. Guinea-pig: a rodent (Hystricomorph).
CEBIDÆ. American monkeys (Platyrrhines): a family of Primates.
CEBUS. Capuchin monkey: a primate (Cebidæ).
CENTROPHORUS CALCEUS. Deep-sea shark: a selachian fish.
CENTROSTEPHANUS LONGISPINUS. Sea-urchin: an echinoderm (Echinoidea), **117**
CEPHALASPIS. Extinct agnathous fish, **234**
CEPHALOCHORDATA (Acrania). A sub-phyllum of chordates, comprising the lancelets.
CEPHALOPODA. A class of molluscs, comprising octopus, squid, nautilus, etc.
CERATOPOGON. A midge: dipterous insect.
CERCOCEBUS. Mangabey of Africa: a primate (Cebidæ).
CEREOPSIS. Australian goose: Anseriformes.
CERVUS PORCINUS. Hog-deer: a ruminant.
CESTODA. A class of unsegmented worms comprising the parasitic tape-worms.

- CETACEA. An order of mammals, comprising the whales and dolphins.
- CETOMIMUS. A deep-sea teleostean fish.
- CETONIA. Rose-chaffer: a coleopterous insect, 219
- CHÆTOGNATHA. Arrow-worms: a phylum of invertebrates.
- CHÆTOPTERUS. A sedentary polychæte worm.
- CHAMÆLEON. The chameleon: reptile of the lizard family.
- CHANOS. Milk-fish: a clupeid teleostean fish.
- CHARAX. Sea-bream: a teleostean fish.
- CHARINA. Rubber-boas: a boid snake.
- CHARYBDEA. A jelly-fish: cœlenterate (Scyphozoa).
- CHELIDON. Martinet, a common European martin: passerine bird of the swallow family.
- CHELODINA LONGICOLLIS. Murray turtle: a chelonian reptile.
- CHELONIA MYDAS. The green or edible turtle: a chelonian reptile.
- CHELONIA. An order of reptiles, comprising the tortoises and turtles.
- CHELONIDÆ. A family of chelonians comprising the marine turtles.
- CHELYDRA SERPENTINA. The alligator terrapin (snapping turtle): a chelonian reptile.
- CHILOPODA. An order of myriapods, comprising the centipedes.
- CHIMÆRA MONSTROSA. Rabbit-fish: a holocephalian fish.
- CHINCHILLA. The chinchilla: a rodent (Hystricomorpha).
- CHIRONOMUS. A dipterous insect.
- CHIROPTERA. An order of mammals comprising the bats.
- CHITON. "Coat-of-mail": a mollusc (Placophora), 196
- CHLAMYDOSAUROS. Frilled lizard: an agamid lizard, 356
- CHOLÆPUS DIDACTYLUS. Two-toed sloth: Xenarthra (Bradypodidæ), 607
- CHOLOGASTER. Kentucky cave-fish: a teleostean fish (Amblyopsidæ).
- CHONDRICTHYES. Class of cartilaginous fishes comprising the selachians and holocephalians.
- CHONDROSTEI. A sub-class of bony fishes comprising the sturgeons and Polypterini.
- CHORTIPPUS. A grasshopper: insect (Orthoptera).
- CHRYSEMYS PICTA. Painted terrapin: a chelonian reptile.
- CHRYSOCHLORIS. Golden mole: a mammal (Insectivore), 442
- CHRYSOPS MARMORATUS. Horse-fly: a dipterous insect (Tabanidæ).
- CHRYSOTIS. Green parrot: Psittaciformes
- CHTHONIUS ISCHNOCHULES. A pseudo-scorpion: Arachnida, 215
- CICHLA. A cichlid: fresh-water teleostean fish, 291
- CICINDELA. Tiger beetle: a coleopterous insect.
- CICONIIFORMES. An order of water birds comprising herons, spoonbills, storks, etc.
- CILIATA. Order of Protozoa comprising *Paramœcium*, *Stentor*, etc.
- CILIOPHORA. A class of Protozoa comprising Ciliata and Suctorina.
- CINYXIS EROSA. Pitted hinged tortoise: a reptile.
- CIONA. A protochordate (Tunicata).
- CIRRIPIEDIA. An order of crustaceans, comprising barnacles, acorn-shells, etc.
- CIRROTHAUMA MURRAYI. A blind deep-sea octopod: cephalopod mollusc.
- CISTELLA. A lamp-shell: Brachiopod.
- CITELLUS CITELLUS. Squirrel (ground squirrel): a rodent (Sciuridæ).
- CLADOCERA. Sub-order of branchiopod crustaceans comprising the water fleas.
- CLADOPHORA. An alga: a thallophyte.
- CLEMMYS. Terrapin (water-tortoise): a chelonian reptile, 682.
- CLETHRIONOMYS. Red backed vole: a rodent (mouse family).
- CLUPEA HARENGUS. Herring: a clupeid teleostean fish, 299
- C. PILCHARDUS. Sardine.
- CLUPEIDÆ. Family of teleostean fishes including herrings, anchovies, etc.
- CNIDARIA. Sub-phylum of stinging cœlenterates, including jellyfish, sea-anemones, etc.
- CÆLACANTHINI. Sub-class of bony fishes, with a single extant species—*Latimeria*.
- CÆLENTERATA. The phylum comprising jellyfish, hydroids, sea-anemones, etc.
- COLAPTES. A woodpecker (flicker): bird of the family Picidæ, 420.
- COLEONYX. A gecko: a reptile of the lizard family.
- COLEOPTERA. An order of insects comprising the beetles.
- COLLEMBOLA. An order of primitive, wingless insects comprising the springtails.

COLUBER GUTTATUS. Corn snake: a colubrid snake.

COLUBRIDÆ. The largest family of snakes, containing the cobras, grass snakes, rattlesnakes, etc.

COLUMBA. Pigeon: Columbidae.

C. LIVIA. Rock-dove, from which domestic pigeons originated.

C. PALUMBUS. Wood-pigeon or ring dove.

COLUMBIDÆ. Family of birds comprising the pigeons and doves.

CONOLOPHUS SUBCRISTATUS. Galapagan iguanid lizard: a reptile.

CONSTRUCTOR CONSTRUCTOR. Common boa: a S. American boid snake.

COPEPODA. An order of free-swimming, planktonic, or parasitic crustaceans, comprising *Copilia*, *Cyclops*, *Caligus*, etc.

COPILIA. A free-swimming copepod crustacean, 209

CORDYLOSaurus. A lizard: lacertilian reptile.

COREPHIUM. A placophoran mollusc.

CORVIDÆ. The crow family of birds: Passeriformes.

CORVUS MONEDULA. A jackdaw: crow family.

CORICEUS. A copepod crustacean.

COTTUS BUBALIS. Bull-head: a teleostean fish.

CRAGO (*CRANGON*). Common shrimp: a decapod crustacean, 205

CRENILABRUS. A teleostean fish.

CRIBRINA. A sea-anemone: cœlenterate (Anthozoa).

CRINOIDEA. A class of Echinoderms, comprising sessile sea-lilies and free-swimming feather stars.

CROCODYLIA. An order of reptiles comprising the crocodiles, alligators, gavials.

CROCODYLUS. Crocodile: a reptile, 378.

C. POROSUS. Salt-water (estuarine) crocodile.

CROSSOPTERYGII. A sub-group of bony fishes, the modern representatives of which are the Dipnoans, but from which were derived the Amphibians, Reptiles, Birds and Mammals.

CROTALIDÆ. A family of viperine snakes comprising the pit vipers (rattlesnakes, moccasin, etc.).

CROTALUS. Rattlesnake: crotalid snake.

CROTAPHYTUS. A lizard: lacertilian reptile.

CRUSTACEA. A class of Arthropoda comprising the larger crabs, lobsters, etc., and the small water-fleas, copepods, etc.

CRYPTOBRANCHUS. "Hellbender", American salamander: a urodelan amphibian.

CRYPTOTYMPANA. A cicada: hemipterous insect.

CTENOPHORA. A class of non-stinging cœlenterates comprising the comb-jellies.

CULEX. A mosquito: dipterous insect.

CUNICULUS. Spotted cavy (paca): a rodent (Hystricomorph).

CRANOCITTA. Blue-jay: a passerine bird of the crow family, 414

CYCLODORIPPE. A deep-sea crustacean.

CYCLOPS. A fresh-water copepod crustacean, 152

CYCLOSA INSULANA. A Malayan spider: arachnid (Araneida).

CYCLOSTOMATA. An extant sub-class of the agnathous fishes, comprising the lampreys and hag-fishes.

CFYMONOMUS. A deep-sea crustacean.

CYNICTIS. A viverrine carnivore of the mongoose family.

CYNOMYS. Prairie-dog: an American burrowing rodent of the squirrel family.

CYPRIDINA. Salt-water ostracod crustacean.

CYPRINIDÆ. The family of teleostean fishes comprising the carp, minnow, goldfish, etc.

CYPRINUS CARPIO. The carp: cyprinoid teleostean fish, 291

CYPRIS (*CYPRIA*). Fresh-water ostracod crustacean, 152, 208

CYSTOFLAGELLATA. Planktonic flagellate Protozoa.

DACELO GIGAS. Laughing jackass (Australian kingfisher): Alcedinidæ.

DACTYNOTUS OBSCURUS. An aphid: hemipterous insect (Aphididæ), 224

DAFLA ACUTA. Pintail duck: Anseriformes (Anatidæ).

DAPHNIA. Water-flea: a branchiopod crustacean (Cladocera), 74, 208

- DASYCHONE*. Tubicolous polychæte worm.
- DASYFELTIS SCABRA*. The egg-eating snake: an African colubrid snake, 392
- DASYPUS*. Armadillo: *Xenarthra* (Dasypodidæ), 442
- DASYURUS*. Australian native cat or dasyure: marsupial (Dasyuridæ), 438
- DECAPODA. An order of larger crustaceans, comprising the lobster, shrimp, crab, etc.
- DELPHINUS*. The dolphin: a small toothed whale, 444
- DEMODEX FOLLICULORUM*. Follicle mite: an arachnid (Acarina).
- DENDROCELUM*. Flat-worm: a turbellarian (Tricladida), 188
- DENDROCOPIUS MAJOR*. Great spotted woodpecker: Picidæ, 414
- DENDROCYGNA*. Tree-duck: Anseriformes (Anatidæ).
- DENTALIUM*. Elephant's tooth shell: scaphopod mollusc, 197
- DERMAPTERA. An order of insects, comprising the earwigs.
- DERMOCHELYS CORIACEA*. Leathery skinned turtle: a chelonian reptile.
- DERMOPTERA. An order of mammals comprising the flying lemurs.
- DESMODUS*. Vampire bat: Chiroptera.
- DIADEMA*. A sea-urchin: echinoderm (Echinoidea), 185
- DIALOMMUS FUSCUS*. Four-eyed blenny: a teleostean fish.
- DICOTYLES*. Peccary: Artiodactyl (pig family), 458
- DIDELPHYS VIRGINIANA*. Virginian opossum: American marsupial, 439
- DINEUTUS*. A whirligig beetle: coleopterous insect (Gyrinidæ).
- DINOFLAGELLATA. Planktonic flagellate Protozoa, 179
- DINOPHILUS*. A marine archiannelid worm.
- DIOMEDEA CAUTA*. Albatross, the largest of the sea-birds, related to the petrels: Procellariiformes, 418
- DIPLOPODA. An order of Myriapoda, comprising the millipedes.
- DIPNOI. A sub-class of bony fishes, comprising the lung-fishes.
- DIPTERA. An order of insects comprising the true flies.
- DISPHOLIDUS*. A colubrid snake: Ophidia.
- DIXIPPUS*. Stick-insect: an orthopterous insect, 218
- DOLICHOPTERYX*. A deep-sea teleostean fish.
- DOLICHOTIS PATAGONICA*. Patagonian cavy: a rodent (Hystricomorph).
- DORYLUS*. An African driver-ant: a blind hymenopterous insect (Formicoidea).
- DREPANOPHORUS*. A nemertine worm.
- DROMÆUS*. The emu: a flightless bird (Ratitæ), 397
- DROSOPHILA*. The fruit-fly: a dipterous insect, 44
- DRYOPHIS*. Long-nosed tree-snake: a reptile.
- DRYOPHIOPS*. A relative of *Dryophis*.
- DYTISCUS MARGINALIS*. Carnivorous water-beetle: a coleopterous insect, 168
- ECHINODERMATA. A phylum of invertebrates, comprising starfishes, sea-urchins, feather-stars, etc.
- ECHINOIDEA. A class of echinoderms (sea-urchins).
- EDENTATA. A former title for three orders of mammals—*Xenarthra*, *Pholidota* and *Tubulidentata*.
- EISENIA FOETIDA*. The dung-heap earthworm: an oligochaete worm.
- ELAPHE QUADRIVITTATA*. Chicken snake: a colubrid snake.
- E. QUATORLINEATA*. Four-line snake.
- ELAPIDÆ. A family of venomous snakes, including the cobras, coral snakes, tiger snakes, etc.
- ELAPS. Coral-snake: an elapid snake.
- ELATERIDÆ. A family of beetles comprising the click-beetles (fire-beetles): Coleoptera.
- ELECTROPHORUS ELECTRICUS*. The electric eel: a teleostean fish.
- ELEDONE*. An octopod: cephalopod mollusc, 146
- ELAPHAS MAXIMUS*. The Indian elephant: Proboscidea.
- ELIOMYS*. A dormouse: a myomorph rodent (Gliridæ).
- ELLOBIUS*. A rodent mole: mouse family.
- ELYSIA*. A marine gastropod mollusc (Opisthobranch).
- EMPLECTONEMA KANDAI*. A luminous, marine, nemertine worm.
- EMYDA*. Soft-shelled turtle: a chelonian reptile.

- EMYDA GRANOSA*. Burgoma soft-shelled turtle.
- EMYS*. Fresh-water tortoise: a chelonian reptile (Testudinidæ).
- E. ORBICULARIS*. European pond tortoise.
- ENCHELIOPHIS JORDANI*. Pearl-fish: the larval form of *Fierasfer* which is parasitic in sea-cucumbers or bivalves: a teleostean fish of the blenny family.
- ENGRAULIS*. The anchovy: a clupeid teleostean fish.
- ENTOSPHECUS*. A lamprey: cyclostome.
- EPHEMEROPTERA*. An order of insects comprising the mayflies.
- EPHESTIA*. The flour-moth: lepidopterous insect, the larvæ of which feed on flour.
- EPICRATES*. A tree-boia: a non-poisonous boïd snake.
- EPINEPHELUS*. Grouper fish: a teleostean fish of the sea-bass family, 92
- EPOMOPHORUS*. An Ethiopian fruit-bat: Megachiroptera.
- EPTATRETUS*. The Chilean borer, a slime-hag: myxinoid cyclostome.
- EQUUS (ASINUS) ASINUS*. Ass (donkey): Equidæ.
- E. CABALLUS*. The domestic horse.
- E. PRZEWALSKII*. Prejvalski's horse (a wild horse of Asia), 686
- E. SOMALIENSIS*. Somali wild ass, 686
- E. ZEBRA*. The zebra, 444
- ERAX RUFIBARBS*. A robber-fly: dipterous insect.
- EREMIAS*. A desert lizard: reptile (Lacertidæ).
- ERICYMBA*. Silverjaw minnow: a cyprinoid teleostean fish.
- ERINACEUS*. Common genus of hedgehog: an insectivorous mammal, 442
- ERISTALIS*. Drone-fly: a dipterous insect.
- ERITHACUS RUBECULA*. European robin: a passerine bird (thrush family).
- ERRANTIA*. A division of polychæte worms comprising the free-swimming types (such as *Nereis*) in contrast to the Sedentaria.
- ERYX*. Sand-boia: a boïd snake.
- ESOX LUCIUS*. The northern pike: teleostean fish (Esocidæ).
- ETMOPTERUS*. A deep-sea luminous shark: selachian fish.
- ECCALIA*. A stickleback: teleostean fish.
- ECDESDRIUM*. A hydrozoan cœlenterate.
- EDDYPTES CRISTATUS*. Rock-hopper penguin: aquatic bird (Impennes), 408
- EUGLENA*. Flagellate protozoon which forms green scum on stagnant water, 179
- ECNICE*. A free-swimming polychæte worm.
- EUPAGURUS*. A hermit-crab: decapod crustacean, 58
- EUPHAGUS CYANOCEPHALUS*. A blackbird: passerine bird (thrush family).
- EUPOLYDONTES*. A pelagic free-swimming polychæte worm.
- EUPROCTIS*. Tussock moth: lepidopterous insect (Lymantrid).
- EURYPTERIDA*. An extinct order of aquatic arthropods, related to the arachnids (particularly the king-crabs), 157
- EUSELACHII*. A sub-class of selachian fishes, comprising the sharks and dogfishes.
- EVARCHA BLANCARDI*. A jumping spider: arachnid (Araneida: Salticidæ), 580
- EVERMANELLA*. A deep-sea teleostean fish.
- FABRICIA*. A free-swimming polychæte worm.
- FALCO*. Falcon: a bird-of-prey (Falconiformes).
- F. TINNUNCULUS*. The kestrel.
- FALCONIFORMES*. An order of birds, comprising the birds-of-prey (eagle, hawk, vulture, etc.)
- FASCIOLA HEPATICA*. The liver-fluke: a trematode worm, 189
- FELIS DOMESTICA*. Cat: a carnivore (Felidæ).
- F. LEO*. The lion.
- F. LIBYCA*. The bush-cat.
- F. LYNX*. The lynx, 444.
- F. ONCA*. The jaguar.
- F. PARDUS*. The leopard.
- F. TIGRIS*. The tiger.
- FISSIPEDIA*. A sub-order of mainly terrestrial carnivores, comprising the cat, dog, bear families, etc.

FITZROYA LINEATA. A teleostean fish.

FLAGELLATA. A class of Protozoa with undulating flagella, comprising *Euglena*, *Volvox*, *Noctiluca*, etc.

FORAMINIFERA. An order of rhizopod Protozoa having a calcareous shell, 179

FORFICULA. The common earwig: an insect (Dermaptera), 218

FULICA. The coot: an aquatic bird (Ralliformes).

FULMAREUS GLACIALIS. The fulmar petrel; an aquatic bird (Procellariidae).

FUNDULUS. Killifish: a cyprinodont teleostean fish, 308

GADUS MORRHUA. The codfish: a teleostean fish (Gadidae), 299

GALAGO. The bush-baby: a nocturnal lemuroid (Primate).

GALEORHINUS. The school shark: a selachian fish.

GALLIFORMES. An order of birds, comprising the game-birds (chicken, pheasant, grouse, etc.).

GALLUS DOMESTICUS. Domestic fowl: Galliformes.

GAMMARUS. A fresh-water shrimp: amphipod crustacean.

GARRULUS. The jay: a passerine bird of the crow family.

GASTEROSTEUS ACULEATUS. Three-spined stickleback: a teleostean fish, 84

GASTROPACHA RUBI. A lappet moth: lepidopterous insect.

GASTROPODA. A class of molluscs comprising the snails, whelks, limpets, etc.

GAVIA. The diver or loon: a fish-eating diving bird (Colymbiformes).

GAZELLA. The gazelle: a ruminant (Bovidae) of the antelope family, 444

GEKKO GEKKO. A gecko: lacertilian reptile (Geckonidae).

GELASIMUS ARCUATUS. A fiddler-crab: decapod crustacean, 205

GEONEMERTES. A terrestrial nemertine worm.

GEOPLANA MEXICANA. A planarian worm: Turbellaria (Tricladida), 188

GEOTRIA AUSTRALIS. A lamprey: cyclostome.

GEOTRUPES. The dung-beetle: a coleopterous insect, 61

GERANOÆTUS. The Chilean eagle: a bird-of-prey (Falconiformes), 398

GERRHONSAURUS GRANDIS. African plated lizard: a lacertilian reptile.

GIGANTACTIS. Angler-fish: a deep-sea teleostean fish.

GIGANTURUS CHUNI. Giant-tailed fish: a deep-sea teleostean fish, 322

GILLICHTHYS MIRABILIS. Mud-sucker: a goby fish (Teleost).

GINGLYMOSTOMA. Nurse shark: a selachian fish.

GIRAFFA CAMELOPARDALIS. The giraffe: a ruminant, 444

GIRELLA. Sea-bream: a teleostean fish.

GLOSSINA. The tsetse-fly: a dipterous insect (Muscidae), 45

GobiUS. A goby-fish: small marine teleostean fish (Gobiidae), 296

GONATODES FUSCUS. A gecko: lacertilian reptile (Geckonidae).

GONEPTERYX RHAMNI. A butterfly: lepidopterous insect.

GONIUM. An alga: a thallophyte.

GONODACTYLUS. A stomatopod crustacean, 60

GONYAULAX. A dinoflagellate protozoon, 179

GORILLA GORILLA. The gorilla: an anthropoid ape (Primate).

GRUS. The crane: a long-legged bird (Gruiformes).

GULO LUSCUS. The wolverine: a badger-like carnivore (Mustelidae).

GYMNOTHORAX. The Moray eel: a teleostean fish.

GYMNURA. The rat-shrew: an insectivore of the hedgehog family.

GYRINIDÆ. The aquatic, carnivorous whirligig beetles: Coleoptera.

HEMADIPSA. A land leech: an annelid (Hirudinea), 190

HEMOPIS. A horse-leech: an annelid (Hirudinea).

HAIDETORITON. A blind salamander: urodelan amphibian.

HALIAETUS LEUCOCEPHALUS. The bald sea-eagle: a bird-of-prey (Falconiformes), 410

HALICORE (DUGONG). The dugong or sea-cow: a sirenian mammal.

HALIOTIS. Ear-shell or abalone: a gastropod mollusc (Prosobranch).

HAPALEMUR. A Madagascan lemur: Primate (Lemuridae).

HAPALIDÆ. A family of New World monkeys, comprising the marmosets.

HATTERIA. See SPHENODON.

- HELIODRILUS*. An oligochaete worm.
- HELIX*. The common genus of snail: a gastropod mollusc (Pulmonate), 142
- H. ASPERSA*. Garden snail.
- H. POMATIA*. Edible (Roman) snail.
- HELODERMA*. The Gila monster: a poisonous lizard of Mexico and Arizona, 359.
- HELOPHILUS*. The hover-fly: a dipterous insect, 141
- HEMICHORDATA. A sub-phylum of the Protochordata, including *Balanoglossus*.
- HEMICHROMIS BIMACULATUS*. A jewel fish (spotted cichlid): teleostean fish.
- HEMIDACTYLUS*. A nocturnal gecko: lacertilian reptile (Geckonidae), 629
- HEMIMYSIS*. A mysid (opossum shrimp): schizopod crustacean.
- HEMIPTERA. An order of insects, comprising the bugs—Homoptera (cicadas, aphids, etc.), and Heteroptera (bed-bug, *Notonecta*, etc.).
- HERPESTES*. The mongoose: a viverrine carnivore, 472
- HETERODON MADAGASCARIENSIS*. Madagascar sharp-nosed snake: a reptile.
- HETERODONTUS PHILLIPPI*. Port Jackson shark: a selachian fish, 286
- HETEROPODA. A class of pelagic gastropod molluscs (Prosobranchs), including *Pterotrachea*, *Carinaria*, etc.
- HETEROTEUTHIS*. A deep-sea luminous squid: cephalopod mollusc.
- HIODON*. "Moon-eye": a fresh-water teleostean fish.
- HIPPOCAMPUS*. The sea-horse: a teleostean fish, related to pipe-fish, 310
- HIPPOLYTE VARIANS*. The chameleon prawn: a decapod crustacean, 91
- HIPPOPOTAMUS*. The hippopotamus: an artiodactyl of the pig family (Suidae).
- HIRUDINEA. The leech family: annelid worms.
- HIRUDO MEDICINALIS*. The medicinal leech, 193
- HIRUNDO RUSTICA*. The chimney swallow: a passerine bird, 414
- HOLOCEPHALIA. A sub-class of the cartilaginous fishes comprising the chimæras.
- HOLOSTEI. A sub-class of bony fishes, comprising the gar-pike and the bowfin.
- HOLOTHURIA*. A sea-cucumber: echinoderm (Holothuroidea), 185
- HOLOTHUROIDEA. A class of Echinodermata, comprising the sea-cucumbers.
- OMALOPSINÆ. A sub-family of colubrid snakes, comprising some species of river-snake.
- HOMARUS VULGARIS*. The common lobster: a decapod crustacean, 206
- HYÆNA*. The hyæna: a nocturnal carnivore (Fissipede), 414
- H. BRUNNEA*. Brown hyæna.
- H. STRIATA (HYÆNA)*. Striped hyæna.
- HYDRA*. A fresh-water polyp: hydrozoan cœlenterate, 182
- HYDRACARINA (HYDRACHNIDA). Water-mites: a family of Acarina.
- HYDROCHERUS CAPTARA*. The capybara: the largest of the rodents (Hystricomorpha).
- HYDROID. Colonial polyp stage of a hydrozoan cœlenterate, from which free-swimming medusoids are liberated.
- HYDROIDES*. A genus of polychæte worm.
- HYDROPHINÆ. A sub-family of the Elapidae, comprising the sea-snakes.
- HYDROZOA. A class of cœlenterates, consisting of the solitary and colonial polyps and medusoids.
- HYGROBATES*. A fresh-water mite: Hydracarina.
- HYLA ARBOREA*. European tree-frog: an anuran amphibian (Hylidae), 341
- H. CÆRULEA*. Australian green tree-frog.
- H. VASTA*. Giant tree-frog of Haiti.
- HYLOBATES*. The gibbon: an anthropoid ape (Primate).
- HYMENOLEMUS MALACORHYNCHUS*. New Zealand blue duck: Anseriformes (Anatidae).
- HYMENOPTERA. An order of insects comprising the bees, ants, wasps (Aculeata), and the sawflies, ichneumon flies, etc.
- HYORIUS*. A Japanese salamander: urodelan amphibian.
- HYPEROÖDON*. The beaked or bottle-nosed whale: a cetacean (Odontoceti).
- HYPNARCE*. An electric ray: selachian fish.
- HYPOGEOPHIS*. A cæcilian amphibian.
- HYPODACHUS INCRASSATUS*. An American toad: an anuran amphibian.
- HYPSIGLENA*. Spotted night snake: a colubrid snake.
- HYPSIPRYMNUS RUFESCENS*. Rufous rat-kangaroo: a marsupial (Macropodidae).

HYRACOIDEA. An order of mammals comprising the coneys or hyraxes.

HYSTRICOMORPHA. A sub-order of rodents, comprising the porcupines, caviés, chinchilla, etc.

HYSTRIX CRISTATA. The Old World porcupine: a hystricomorph rodent, 442

ICHTHYOMYZON. American fresh-water lamprey: a cyclostome.

ICHTHYOPHIS. A cæcilian amphibian, 730

ICHTHYOPSIDA. A group of vertebrates comprising the fishes and amphibians (contrasted with the Sauropsida and Mammalia).

IDIACANTHUS. A deep-sea teleostean fish, the larva of which is *Stylophthalmus*, 328

IDOTEA. Beach-louse: an isopod crustacean.

IGUANA. A large, crested American lizard: lacertilian reptile (Iguanidæ), 358

I. TUBERCULATA. Tuberculated iguana of W. Indies.

IMAGO. A sexually mature adult insect.

IMPENNES (Sphenisciformes). A family of birds comprising the penguins.

INDRIS. A Madagascan lemur: Primate (Lemuroidea).

INSECTIVORA. A primitive order of mammals, comprising the hedgehogs, moles, shrews, etc.

IPNOPS. A blind deep-sea teleostean fish, 724

ISOPTERA. An order of insects comprising the termites.

ISTIOPHORUS. Sail-fish: a pelagic teleostean fish, related to swordfish.

IXODIDES. A sub-order of Acarina, comprising the ticks.

JULIS. A wrasse: teleostean fish (Labridæ).

JULUS. A millipede: myriapod (Diplopoda).

JUNCO HYMENALIS. An American finch: a passerine bird (finch family).

KALOULA PULCHRA. Malayan bull-frog: an anuran amphibian.

LABRUS. A wrasse: teleostean fish (Labridæ).

LACERTA. The common genus of lizard: a reptile.

L. MURALIS. The wall-lizard, 355

L. VIRIDIS. The green lizard.

L. VIVIPARA. The common English lizard.

LACERTILIA. A sub-order of reptiles comprising the lizards (geckos, chameleon, slow-worms, etc.).

LEMAROUS. Greenland shark: a selachian fish, 281

LAGOMORPHA. The family of rodents (or, more recently, a separate order of mammals), comprising the rabbits and hares, and the pikas.

LAGOPUS MUTUS. The ptarmigan: a bird of the northern and mountainous regions (grouse family).

LAGOSTOMUS. The vizcacha: a hystricomorph rodent, 442

LAMA. The llama (alpaca, vicugna) of S. America: an artiodactyl (Tylopoda), relative of the camel, 444

LAMELLIBRANCHS. See BIVALVES.

LAMNA CORNUBICA. The porbeagle shark: a selachian fish, 283

LAMPANYCTUS. A deep-sea teleostean fish.

LAMPETRA FLUVIATILIS. The river lampern: a cyclostome.

L. PLANERI. The brook lampern.

LAMPROCOLIUS CHALYBEUS. A starling: passerine bird (Sturnidæ).

LAMPROPELTIS GETULUS. The king-snake: a N. American colubrid snake.

LAMPYRIDÆ. A family of beetles including the fire-flies (male) and the wingless glow-worms (female or larva).

LAMPYRIS (*NOCTILUCA* and *SPLENDIDULA*). Fire-flies or glow-worms: Coleoptera (Lampyridæ).

LANIUS. Shrike (butcher bird): a passerine bird (Laniidæ), 662.

LANTHANTUS. A lizard of Borneo, related to *Heloderma*: a reptile.

LARIDÆ. The gull family of birds.

LARUS ARGENTATUS. The herring-gull.

LASIUS. A garden ant: hymenopterous insect (Formicidæ).

- LATIMERIA*. The coelacanth: a bony fish, descended from the crossopterygians, thought to be extinct but recently found off the coast of Africa, **315**
- LATRODECTUS*. A small venomous spider (katipo) of Australasia: arachnid (Araneida), **84**
- LEANDER*. A prawn: decapod crustacean, **578**
- LEBISTES RETICULATUS*. The guppy ("millions fish"): a cyprinodont teleostean fish.
- LEMUR CATTALIA*. The rat-tailed lemur, a "true" lemur of Madagascar: Primate (Lemuroidea).
- LEMUROIDEA*. A sub-order of Primates, comprising the "true" lemurs, and the nocturnal lemuroids (galago, loris, *Nycticebus*, etc.).
- LEOTICHUS GLAUCOPIS*. A cave-bug: a hemipterous insect, **222**
- LEPADOGASTER*. Cling-fish: a carnivorous, marine teleostean fish.
- LEPAS*. The ship-barnacle, with a free-swimming nauplius larva: a cirripede crustacean, **209**
- LEPIDOPTERA*. An order of insects, comprising the butterflies and moths.
- LEPIDOSIREN*. The South American lung-fish: a dipnoan fish, **312**
- LEPIDOSTEUS*. The gar-pike: a holostean fish, **321**
- LEPISMA*. The silver-fish: a primitive, wingless insect (bristletail: Thysanura), **218**
- LEPOMIS*. A sun-fish: a fresh-water teleostean fish.
- LEPTINOTARSA*. Colorado beetle: a coleopterous insect, **219**
- LEPTODEIRA ANNULATA*. A colubrid snake.
- LEPTODORA*. A water-flea: a branchiopod crustacean (Cladocera), **207**
- LEPTOGNATHUS*. The serpent-eel of New Zealand: a teleostean fish.
- LEPTOPLANA*. A leaf-like, marine turbellarian worm (Polycladida), **187**
- LEPCS*. The genus of "true" hare: Lagomorpha.
- L. TIMIDUS*. The varying hare.
- LEUCOSOLENIA*. A sponge: Porifera, **181**
- LIGIA*. A marine isopod crustacean, **95**
- LIMA*. An active bivalve mollusc which swims by moving its shell-valves and mantle-lobes.
- LIMAX*. Grey slug: a gastropod mollusc (Pulmonate), **197**
- LIMNÆA*. A fresh-water snail (pond snail): a gastropod mollusc (Pulmonate), **196**
- LIMNÆA*. A fresh-water mite: acarine (Hydracarina).
- LIMULUS POLYPHEMUS*. N. American king-crab, or horseshoe crab: an arachnid (Xiphosura), **161, 211**
- LINÆUS RUBER*. An aquatic nemertine worm, **189**
- LITHOBIVUS*. A centipede: myriapod (Chilopoda).
- LITTORINA NERITOIDES*. Periwinkle: a gastropod mollusc (Prosobranch), **45**
- LIZZIA*. A hydrozoan coelenterate.
- LOCUSTA MIGRATORIA*. The migratory locust, or grasshopper: Orthoptera (Acrididæ), **69**
- LOLIGO*. Common squid: a dibranchiate cephalopod mollusc, **145**
- LOPHORTYX CALIFORNICUS*. The Californian valley quail: Galliformes (pheasant family), **417**
- LORIS GRACILIS*. The slender loris: a nocturnal lemuroid primate.
- LOTA*. The burbot: a fresh-water teleostean fish (cod family: Gadidæ).
- LOXIA*. The cross-bill: a passerine bird (finch family).
- LOXODONTA AFRICANA*. The African elephant: Proboscidea.
- LUCIFUGA*. Cuban blind cave-fish: a teleostean fish.
- LUCIOPERCA*. The pike-perch: a teleostean fish (Percidæ).
- LUMBRICULUS*. An earthworm: oligochæte worm.
- LUMBRICUS TERRESTRIS*. The common earthworm: oligochæte worm, **190**
- LUTIANUS*. The snapper: a teleostean fish (sea-bass family).
- LUTRA*. The otter: a mustelid carnivore.
- LUTREOLA*. The mink: a mustelid carnivore.
- LYCOSA AGRICOLA*. Wolf-spider: arachnid (Araneida), **214**
- LYCOTEUTHIS DIADEMA*. The "wonder lamp", a luminous, deep-sea squid: dibranchiate cephalopod mollusc, **740**
- LYGODACTYLUS*. A gecko: lacertilian reptile (Geckonidæ).
- LYMANTRIA*. Tussock-moth: a lepidopterous insect.
- LYTECHINUS*. Sea-urchin: an echinoderm (Echinoidea).
- MABUYA*. A genus of skink: lacertilian reptile (Scincidæ).
- MACACA (MACACUS)*. Macaque monkeys: Old World monkeys (Catarrhine).

- MACACA PILEATA*. Toque monkey.
- M. RHESUS*. Rhesus monkey.
- M. SPECIOSUS*. Japanese macaque.
- MACROBRACHIUM*. A genus of fresh-water shrimp: decapod crustacean.
- MACROGLOSSA*. Hawk moth: lepidopterous insect.
- MACRONECTES GIGANTEUS*. Giant fulmar: a sea-bird (Procellariidæ).
- MACROSCOLIDÆ*. The elephant-shrew family: insectivores.
- MAGGOT*. The larva of holometabolous insects, such as flies, 50
- MALACOCEPHALUS*. Grenadier: deep-sea teleostean fish.
- MALACOSTRACA*. A sub-class of the crustaceans, comprising the Decapoda, Amphipoda, Isopoda, etc.
- MALOPTERURUS*. Electric cat-fish: siluroid teleostean fish.
- MALPOLOS*. A genus of colubrid snake: reptile (Ophidia).
- MANATUS*. See *TRICHECHUS*.
- MANDRILLUS*. Mandrill: Old World monkey (Catarrhine).
- MANIS*. The pangolin, or scaly ant-eater: termite-eating mammal (Pholidota), 442
- MANTIS RELIGIOSA*. The praying mantis: an orthopterous insect (Mantidæ), 589
- MARMOSA*. Mouse opossum: small American marsupial (Didelphyidæ).
- MARMOTA (ARCTOMYS)*. Marmot: member of the squirrel family of rodents, 442
- MARTES*. Marten: mustelid carnivore.
- MARTHASTERIAS*. A genus of starfish: echinoderm (Echinoidea).
- MASTIGOPROCTUS GIGANTEUS*. A whip-tailed scorpion: an arachnid (Pedipalpi).
- MEDUSA*. Free-swimming marine jellyfish: Scyphozoa.
- MEDUSOID*. Free-swimming form of Hydrozoa, liberated by hydroid colonies ("swimming bells").
- MEGABUNUS DIADEMA*. A harvestman: an arachnid (Phalangida).
- MEGACHIROPTERA*. A sub-order of Chiroptera comprising the larger bats, usually frugivorous, such as the flying foxes.
- MEGALOBATRACHUS MAXIMUS*. The Japanese giant salamander, the largest extant amphibian: a urodele, 349
- MEGANTIPHANES*. A genus of deep-sea luminous shrimp: decapod crustacean.
- MEGAPTERA*. Hump-back whale: cetacean (whale-bone whale), 444
- MEGERLIA*. A genus of lamp-shell: Brachiopod.
- MELANERPES ERYTHROCEPHALUS*. Red-headed woodpecker: Picidæ.
- MELANOPLUS*. American migratory locust: orthopterous insect (Acrididæ).
- MELEAGRIS GALLOPAVO*. The American turkey: Galliformes (pheasant family).
- MELES MELES*. The European badger: a mustelid carnivore, 444
- MELOPSITTACUS UNDULATUS*. The budgerigar, an Australian parakeet: Psittaciformes.
- MELURSUS URSINUS*. The Indian sloth bear: a carnivore (Ursidæ).
- MEPHITIS*. A skunk: mustelid carnivore.
- METAZOA*: The sub-kingdom of multicellular animals: a collective name for all animals except Protozoa and Parazoa.
- METOPOCEROS CORNUTUS*. Horned iguana of Haiti: a lacertilian reptile.
- METRIDIUM*. A genus of sea-anemone: anthozoan coelenterate.
- MICROCHIROPTERA*. A sub-order of Chiroptera comprising the smaller bats (vampire bat, *Vespertilio*, etc.).
- MICROCOCCLUS PHOSPHOREUS*. A luminous bacterium.
- MICROPUS APUS*. The European swift: Apodidæ (Micropodidæ), 407
- MICROSPIRA PHOTOGENICA*. A luminous bacterium.
- MICROTUS*. A field vole: myomorph rodent.
- MILVUS*. A kite: bird-of-prey (Falconiformes), 420
- MISGURNUS*. Loach: cyprinoid teleostean fish, 310
- MYEMIOPSIS*. A genus of luminous comb-jelly: a cœlenterate (Ctenophora).
- MOBULIDÆ*. Devil-fish rays: a family of large batoid selachian fishes.
- MONODON*. Narwhal: arctic whale of the family Delphinidæ, the male of which has a long tusk (sometimes called the sea-unicorn).
- MORDACIA*. A genus of sea-lamprey from Chile and Tasmania: a cyclostome.
- MORMYRIDÆ*. The elephant-fish family of teleostean fishes.

- MOTACILLA ALBA*. The white wagtail: a passerine bird, 660
- MUGIL*. Grey mullet: teleostean fish (Mugilidæ).
- MUREX*. A genus of marine gastropod mollusc, juice from the glands of which provided the Tyrian purple dye (Prosobranch), 197
- MUS MUSCULUS*. The house mouse: myomorph rodent (Muridæ).
- MUSCA DOMESTICA*. The house-fly: a dipterous insect (Muscidæ), 172
- MUSTELA ERMINEA*. The stoat or ermine (in its winter white) (in America, a weasel): a mustelid carnivore.
- M. NIVALIS*. The weasel (in England), 472
- M. PUTORIUS*. See *PUTORIUS PUTORIUS*.
- MUSTELIDÆ. A family of carnivores, comprising the otter, badger, stoat, skunk, etc.
- MUSTELUS*. A genus of dogfish or "hound": a selachian fish, 285
- MYA ARENARIA*. The long clam: a bivalve mollusc, 131
- MYLIOBATIS*. Eagle-ray: batoid selachian fish, 283
- MYOCASTOR COYPUS*. The coypu: a South American aquatic rodent, the fur of which is "nutria" (Hystricomorph).
- MYOCALE*. Water-mole, or desman: insectivore (Talpidæ).
- MYOMORPHA. A division of the rodents comprising the rat, mouse, vole, etc.
- MYRIAPODA. A class of Arthropoda comprising the Chilopoda (centipedes) and Diplopoda (millipedes).
- MYRMECOBIUS*. Banded ant-eater: Australian marsupial (Dasyuridæ), 437
- MYRMECOPHAGA*. The giant ant-eater: South American mammal (Xenarthra), 600
- MYSTACOCETI. A sub-order of Cetacea comprising the baleen or whale-bone whales.
- MYTILUS EDULIS*. The edible mussel: a bivalve mollusc, 200
- MYXICOLA ÆTHETICA*. A free-swimming polychæte worm.
- MYXINE GLUTINOSA*. The glutinous hag-fish: a mud-dwelling or parasitic cyclostome, 114, 734
- MYZUS*. A genus of aphid: hemipterous insect (Aphididæ).
- NAJA TRIPUDIANS*. The Indian cobra: a colubrid snake (Elapinae), 386
- NASUA*. The coati: American carnivore (Procyonidæ), 444
- NAUPLIUS*. The larval stage of many marine crustaceans (e.g., barnacles, copepods, etc.).
- NAUTILUS POMPILIUS*. The pearly nautilus: the only extant tetrabranchiate cephalopod mollusc, 139
- NECROPHORUS*. The burying beetle: coleopterous insect, 219
- NECTURUS*. Mud-puppy: urodelan amphibian related to *Proteus*, 439
- NEMATODA. A phylum of unsegmented worms comprising the mainly parasitic round- or thread-worms.
- NEMERTEA. A phylum of unsegmented worms comprising the mainly marine ribbon-worms.
- NEMESTRINUS*. A genus of macaque monkey: Primate (Catarrhine).
- NEOCERATODUS*. A genus of lung-fish of Queensland: dipnoan fish, 312
- NEODIPRION*. A genus of saw-fly: hymenopterous insect (Tenthredinidæ).
- NEREIS*. The rag-worm: free-swimming polychæte worm, 191
- NEUROPTERA. An order of insects comprising the lace-wings, ant-lions, etc.
- NOCTILUCA*. A genus of luminescent dinoflagellate: a flagellate protozoon, 179, 738
- NOTECHIS*. Tiger snake: a genus of crotalid snake (Elapidæ).
- NOTONECTA*. Water-boatman, or water-bug: a genus of hemipterous insect, 73
- NOTORCTES TYPHLOPS*. The Australian marsupial mole, 437
- NOTROPIS*. Shiner: a fresh-water American genus of cyprinoid teleostean fish.
- NUDIBRANCHIA. Sea-slugs: an order of gastropod molluscs, 196
- NUMIDA PUCHERANI*. The guinea-hen: Galliformes (pheasant family).
- NYCTICEBUS*. Slow loris: lemuroid primate.
- NYCTICORAX*. The night heron: Ciconiiformes, 413
- NYCTIPITHECUS (AOTES)*. The night monkey or Douroucoulis: American nocturnal monkey (Cebidæ).
- NYMPH. The immature stage of certain insects which undergo incomplete metamorphosis (e.g., Orthoptera, Hemiptera, etc.).

- OBELIA*. A genus of marine hydroid: hydrozoan coelenterate, 182
- OCHOTONA*. The pika, or calling hare: Lagomorpha.
- OCTOPUS VULGARIS*. The common octopus: a dibranchiate cephalopod mollusc, 93, 202
- OCTYPODA IPPENS*. The racing crab: a decapod crustacean, 205
- ODONATA. An order of insects comprising the dragonflies, with aquatic larvæ.
- ODONTOCETI. A sub-order of cetaceans comprising the toothed whales (sperm-whale, porpoise, dolphin, etc.).
- ODONTOSYLLIS*. The fire-worm: free-swimming polychæte worm.
- ŒDICNEMUS*. Stone curlew: Charadriiformes.
- OKAPIA*. The okapi: ruminant of the giraffe family.
- OLIGOCHÆTES. A class of annelid worms comprising the earthworms, etc.
- OSCHIDIUM*. A genus of pulmonate mollusc.
- ONISCUS*. A woodlouse: terrestrial isopod crustacean.
- ONYCHOPHORA. A class of Arthropoda comprising the caterpillar-like *Peripatus* and its relatives.
- OPHIOPS*. A genus of lizard: lacertilian reptile.
- OPHIOTETTIX LIMOSINA*. Grouse-locust: an orthopterous insect, 223
- OPHISAURUS VENTRALIS*. The American "glass snake": a lacertilian reptile (Anguidæ).
- OPHIUROIDEA. A class of Echinodermata comprising the brittle-stars.
- OPHRYENNA SUPERCILIOSA*. The Yrpha iguana: a lacertilian reptile.
- OPISTHOBRANCHIA. An order of gastropod molluscs comprising the Nudibranchia, sea-hares, etc.
- OPISTHOPROCTUS*. A genus of deep-sea teleostean fish, 324
- ORCA*. The killer-whale: a genus of cetacean (Delphinidæ).
- ORECTOLOBUS*. The carpet shark: selachian fish.
- ORNITHORHYNCHUS*. The duck-billed platypus: Australian monotreme, 430
- ORTHOPTERA. An order of insects comprising the cockroach, stick-insect, locust, etc.
- ORYCTEROPUS*. The aard-vark: a mammal (Tubulidentata), 442
- ORCTOLAGUS*. The rabbit: Lagomorpha (Leporida).
- OSTEICHTHYES. The class of bony fishes, including the Teleostei, Chondrostei, Dipnoi, etc.
- OSTEOLEMUS TETRASPIS*. The broad-fronted crocodile: a reptile.
- OSTRACODA. An order of small, active, mainly fresh-water crustaceans, comprising *Cypris*, etc.
- OTUS BAKKAMÆNA*. The Scops owl: Strigidæ.
- OVIS*. Sheep: Artiodactyl (Bovidæ).
- OXYBELIS*. A genus of tree-snake: a colubrid snake.
- PACHYDACTYLUS MACULATUS*. A gecko: a lacertilian reptile (Geckonidæ).
- PALEMON*; *PALEMONETES*. Prawns: decapod crustaceans.
- PAN SATRUS*. The chimpanzee: an anthropoid ape.
- PANDALUS*. A genus of deep-sea prawn: decapod crustacean.
- PANTODON*. A flying fish of West Africa: a teleostean fish.
- PAPIO*. The baboon of Africa: catarrhine monkey.
- PARACENTROTUS LIVIDUS*. A sea-urchin: an echinoderm (Echinoid).
- PARALICHTHYS ALBIGUTTUS*. An American flounder: teleostean flat-fish (Pleuronectidæ).
- PARAMÆCIUM*. Slipper animalcule: a genus of ciliate Protozoa, 179
- PARAZOA. A sub-kingdom, comprising the sponges, in contrast to Protozoa and Metazoa.
- PARUS*. A titmouse: passerine bird (Paridæ).
- PASSER DOMESTICUS*. The house sparrow: a passerine bird (finch family), 408
- PASSERIFORMES. The largest order of birds comprising mainly small song birds and birds of perching habits (swallow, thrush, finch, Corvidæ, etc.).
- PASSERITA PRASINA*. The emerald tree-snake: a colubrid snake, 674
- PATELLA VULGATA*. The common European limpet: a gastropod mollusc (Prosobranch), 197
- PAUROPUS*. A genus of blind myriapod (Pauropoda).
- PECTEN*. The scallop: a genus of bivalve mollusc which swims by opening and closing its shell-valves, 200
- PECTUNCULUS*. A genus of bivalve mollusc of the family Arcidæ.
- PEDETES*. The Cape jumping hare: sciuriform rodent.

- PEDICULUS*. Body-louse: a parasitic insect (Anoplura), 218
- PEDIPALPI*. An order of Arachnida comprising the whip-tailed scorpions.
- PELAGIA NOCTILUCA*. A luminous jellyfish: a coelenterate (Scyphozoa).
- PELECANUS*. The pelican: fish-eating bird (Pelecanidae), 410
- PELOBATES FUSCUS*. The European spadefoot toad: a burrowing anuran amphibian.
- PELOMYXA*. Amoeboid protozoon: Rhizopoda.
- PERAGALE*. A rabbit-bandicoot: Australian marsupial (Peramelidae), 441
- PERAMELES*. A bandicoot: Australasian marsupial (Peramelidae).
- PERCA FLUVIATILIS*. The European fresh-water perch: a teleostean fish (Percidae).
- PERICHÆTA*. A genus of annelid worm (Oligochaete).
- PERIOPHTHALMUS*. The mud-skipper, amphibious goby-fish: a teleostean (Gobiidae), 326, 694
- PERIPATOPSIS ALBA*. A South African relative of *Peripatus*.
- PERIPATUS*. A genus of Onychophora: a nocturnal, caterpillar-like arthropod, 139, 204
- PERIPLANETA*. An American cockroach: orthopterous insect (Blattidae).
- PERISSODACTYLA*. An order of mammals comprising the odd-toed ungulates—horse, tapir, rhinoceros, etc.
- PERNIS APIVORUS*. The honey-buzzard, a European hawk: bird-of-prey (Falconiformes).
- PERODICTICUS POTTO*. The potto: a nocturnal lemuroid (Lorisidae), 607
- PETAURUS*. Flying phalanger: Australian marsupial (Phalangeridae).
- PETROGALE*. Rock-wallaby: Australian marsupial (Macropodidae).
- PETROMYZON MARINUS*. The sea-lamprey: a cyclostome, 260, 716
- PHALACROCORAX*. Cormorant: aquatic diving bird (Pelecaniformes), 404
- P. BOUGAINVILLE*. Peruvian guano cormorant.
- PHALANGER MACULATUS*. The spotted cuscus (phalanger): an Australian marsupial (Phalangeridae), 438.
- PHALANGERIDÆ*. A family of Australasian marsupials comprising the phalangers, koala, wombat.
- PHALANGIDA*. An order of Arachnida, comprising the small, long-legged "harvestmen".
- PHASCOLARCTUS*. The koala or native bear: Australian marsupial (Phalangeridae), 440
- PHASCOLOMYS*. The wombat: Australian marsupial (Phalangeridae), 441
- PHENOGODES*. Fire-beetle: coleopterous insect (Cantharidae), 739
- PHILANTHUS TRIANGULUM*. A digger wasp: a hymenopterous insect (Sphecidae).
- PHOCA*. A "hair" seal: pinnipede (Phocidae).
- P. BARBATA*. Bearded seal.
- P. GRENLANDICA*. Common arctic, or harp seal.
- P. VITULINA*. Common (harbour) seal, 502
- PHOCÆNA*. The porpoise: a cetacean (Delphinidae).
- PHOCIDÆ*. A family of Pinnipedia comprising the true seals.
- PHENICOPTERUS*. The flamingo: long-necked and long-legged wading bird, 407
- PHOLAS*. A genus of clam, or "piddock": a wood- or rock-boring bivalve mollusc.
- PHOLIDOTA*. An order of mammals comprising the scaly pangolins.
- PHOLIS*. Butter-fish, or gunnel: teleostean fish.
- PHOTINUS*. A genus of fire-fly (or glow-worm): a coleopterous insect (Lampyridae), 219
- PHOTOPHARON*. Lamp-eyed fish: a genus of luminous teleostean fish (sea-bass family).
- PHOTOSTOMIAS GUERNEI*. A deep-sea, luminous teleostean fish.
- PHOTURUS PENNSYLVANICA*. An American fire-fly: a coleopterous insect (Lampyridae).
- PHOXINUS*. A genus of minnow: a cyprinoid teleostean fish, 294
- PHROXIMA SEDENTARIA*. An amphipod crustacean, 160
- PHRYNOMERUS*. A genus of toad: an anuran amphibian.
- PHRYNOSOMA*. The American horned "toad": iguanid lizard, 365
- PHYLLIRHÆ*. "Flowing leaf": a gastropod mollusc (Nudibranch).
- PHYLLOPODA*. A sub-order of branchiopod crustaceans, comprising *Apus*, *Artemia*, etc.
- PHYLLORHYNCHUS*. A genus of colubrid snake: an ophidian.
- PHYLLOURUS MILII*. A gecko: a lacertilian reptile (Geckonidae).
- PHYSETER*. The sperm whale, or cachalot, large toothed whale: a cetacean, 444
- PHYSIGNATHUS*. A genus of water-dragon of Queensland and Cochin China: lacertilian reptile.
- PICIDÆ*. A family of birds comprising the woodpeckers, fliers, wrynecks.
- PIERIS*. Cabbage white butterfly: lepidopterous insect.

- PINNIPEDIA.** A sub-order of carnivores, comprising the aquatic seals, sea-lions and walruses.
- PIPA AMERICANA.** The Surinam toad: an anuran amphibian, 339
- PISCICOLA.** A genus of leech: annelid worm (Hirudinea).
- PITHECIA.** Saki: a genus of platyrrhine monkey (Cebidæ).
- PITHECUS.** Langur, of India: a genus of catarrhine monkey, 607
- PLACODERMS.** An extinct class of fishes with an armour of bony plates, 234
- PLACOPHORA.** A class of ancient, marine molluscs, comprising the chitons.
- PLAGIOSTOMUM.** A genus of marine flat-worm: turbellarian worm.
- PLANARIA.** A group of elongated flat-worms: turbellarian worms (Tricladida).
- PLANES.** A genus of crab: decapod crustacean.
- PLATYHELMINTHES.** A phylum of unsegmented flat-worms, comprising Turbellaria, Trematoda and Cestoda.
- PLATYRRHINES.** The New World monkeys (Cebidæ and Hapalidæ).
- PLECOPTERA.** An order of insects comprising the stone-flies, 218
- PLECOSTOMUS.** A genus of catfish: a South American fresh-water teleostean, related to the siluroids.
- PLEURODELES.** A genus of newt: urodelan amphibian.
- PLEURONECTES FLENS.** The flounder: a teleostean flat-fish.
- P. PLATESSA.** The plaice.
- PLEXIPPUS SINUATUS.** A jumping spider: an arachnid (Araneida, Salticidæ), 212
- PLUSIA GAMMA.** Gamma moth, a European noctuid moth: lepidopterous insect.
- PODARGUS.** Frog-mouth: an Australian bird, related to goat-sucker.
- POLYCELIS.** A genus of turbellarian worm (Tricladida).
- POLYCHÆTES.** A class of annelid worms comprising free-swimming types (Errantia) such as *Nereis*, and tubicolous types (Sedentaria) such as *Branchioma*.
- POLYCLADIDA.** An order of leaf-like Turbellaria, comprising such types as *Leptoplana*.
- POLYIPNUS.** A genus of deep-sea stomiatid teleostean fish.
- POLYDON.** Spoonbill sturgeon of Mississippi: a chondrosteian fish.
- POLYOPHTHALMUS.** A genus of sedentary marine polychæte worm.
- POLYPEDATES (RHACOPHORUS) REINWARDII.** Javanese flying frog: an anuran amphibian.
- POLYPHEMUS.** A genus of water-flea: branchiopod crustacean (Cladocera), 209
- POLYPTERINI.** A group of African chondrosteian fish with two extant genera.
- POLYPTERUS.** The bichir: a chondrosteian fish (Polypterini), 320
- POLYZOA (BRYOZOA).** A phylum of aquatic, plant-like animals—sea-mats, corallines, 194
- POMOLOBUS.** Skip-jack: a genus of clupeid teleostean fish.
- PONGO.** The orang-utan: anthropoid ape.
- PONTELLOPSIS REGALIS.** A copepod crustacean.
- POPILLIA.** A Japanese beetle: coleopterous insect.
- PORICHTHYS.** Toadfish, Californian stinging fish: a teleostean fish.
- PORIFERA.** A phylum of multicellular, sedentary, aquatic animals—the sponges.
- PORTHESIA.** A genus of tussock moth: lepidopterous insect (Lynantrid).
- PORTUNUS.** Swimming crab: a genus of decapod crustacean.
- POTAMILLA.** A genus of tubicolous polychæte worm.
- POTAMOGALE.** Otter-shrew: aquatic insectivore.
- POUCHETIA.** Dinoflagellate: a genus of flagellate Protozoa.
- PRISTIS.** Saw-fish: shark-like batoid selachian fish, 279
- PROBOSCIDEA.** An order of mammals comprising the elephants, formerly included in the Ungulata.
- PROCAVIA.** Rock hyrax or coney: a distant relative of the elephant (Hyracoidea).
- PROCELLARIA PELAGICA.** Storm petrel (Mother Carey's chickens): an oceanic bird (Procellariidæ), 420
- PROCTACANTHUS.** Robber-fly: a genus of dipterous insect.
- PROCTON.** The raccoon of North America: a genus of Fissipedia (Procyonidæ), 444
- PROCYONIDÆ.** A family of carnivores, comprising the raccoon, panda, coati, etc.
- PROPTHECUS.** Sifaka, a genus of Madagascar lemur: Primate (Lemuroidea).
- PROSOBRANCHIA.** A sub-class of gastropod molluscs comprising the aquatic limpet, whelk, periwinkle, etc.
- PROSTOMA.** A genus of fresh-water ribbon-worm: Nemertine.

- PROTEUS ANGUINUS*. The olm, a cave salamander: urodelan amphibian, **726**
- PROTOCHORDATES. Primitive chordates, comprising Hemichordata, Tunicata and Cephalochordata.
- PROTOPTERUS*. A lung-fish of West Africa: a genus of dipnoan fish, **312**
- PROTOZOA. A phylum comprising the lowest and simplest unicellular animals, mainly aquatic, such as *Amaba*, *Euglena*, malaria parasite, etc.
- PROTURA. An order of minute insects, lacking wings, eyes and antennæ.
- PSEPHURUS*. Sword-bill sturgeon found in the Yangtze-Kiang, China: a chondrosteian fish.
- PSETTODES*. A genus of flounder: a teleostean flat-fish (Pleuronectidae), **329**
- PSEUDOSCORPIONIDEA. An order of Arachnida comprising the book-scorpions, minute animals resembling scorpions but without long tail and sting.
- PSYLLA*. Jumping plant-louse: a genus of hemipterous insect.
- PTERASPIS*. An extinct agnathous fish, **234**
- PTEROCERA LAMBIS*. Spider- or scorpion-shell: a gastropod mollusc, **198**
- PTEROIS*. Lion-fish of tropical Pacific: a poisonous teleostean fish (Scorpenidae).
- PTEROMYS*. Flying squirrel: an Asiatic rodent (Sciuridae).
- PTEROPUS*. Flying fox: a genus of fruit-eating bat (Megachiroptera), **442**, **607**.
- PIEROBRACHIA*. A shell-less heteropod: a genus of gastropod mollusc.
- PTYCHODERA*. A balanoglossid: hemichordate.
- PUFFINUS PUFFINUS*. Manx shearwater: an oceanic bird (Procellariidae), **407**
- PULEX IRRITANS*. The human flea: a blood-sucking insect (Aphaniptera), **219**
- PULMONATA. A sub-class of gastropod molluscs comprising the terrestrial snails and slugs and fresh-water snails.
- PUTORIUS FURIO*. The ferret: a mustelid carnivore.
- P. PUTORIUS*. The polecat, **441**.
- PYCNOGONIDA. An order of Arachnids comprising small marine animals—"sea-spiders", **217**.
- PYGOPUS LEPIDOPUS*. Scale-footed lizard: a snake-shaped lizard of Australasia, without forelimbs.
- PYROPHORUS*. A genus of fire-fly: coleopterous insect (Elaterid).
- PYROSOMA*. A luminous, floating colonial tunicate of tropical seas.
- PYRRHULA*. Bullfinch: a genus of passerine bird (finch family).
- PYTHON*. Python: a genus of boïd snake.
- P. MOLURUS*. Indian python.
- P. REGIUS*. West African python.
- P. RETICULATUS*. Reticulated python of Malaya.
- RADIOLARIA. An order of rhizopod Protozoa with a horny or siliceous skeleton, **179**
- RAJA*. Ray: a genus of batoid selachian fish, **287**
- R. BATIS*. The skate.
- R. CLAVATA*. Thornback ray, **280**
- R. MONTAGUI (MACULATA)*. Spotted ray, **280**
- RANA*. The common genus of frog: an anuran amphibian, **335**
- R. CATESBIANA*. Bull-frog.
- R. ESCULENTA*. Edible water-frog.
- R. PIPIENS*. Leopard frog, **342**
- R. TEMPORARIA*. Common European frog.
- RANATRA*. Water-scorpion: a genus of hemipterous insect (Nepid).
- RANZANIA TRUNCATA*. Truncated sun-fish: a teleostean fish.
- RATITÆ (PALÆOGNATHÆ). Running birds, such as kiwi, ostrich, emu, etc.
- RATTUS*. Rat: a genus of myomorph rodent (Muridae).
- RHACOPHORUS LEUCOMYSTAX*. Malayan "flying" tree-frog: an anuran amphibian (Ranidae).
- RHAMDIA*. A genus of cavernicolous catfish: siluroid teleostean fish.
- RHEA*. South American ostrich or rhea: flightless bird (Ratitæ), **410**
- RHINEURA FLORIDANA*. Florida worm lizard: a limbless burrowing reptile.
- RHINOCEROS*. The rhinoceros—a large perissodactyl of Asia and Africa, **444**.
- RHINOGLENA*. A wheel-animalcule—a genus of rotifer.
- RHINOPIHIS*. A burrowing snake of India: a genus of uropeltid snake.
- RHIZOPODA (SARCODINA). A class of mainly amœboid Protozoa.

RHYTINA (*HYDRODAMALIS*) *STELLARI*. Steller's sea-cow: an extinct sirenian.

ROTIFERA. A phylum of beautiful, microscopic, aquatic animals—wheel-animalcules, 194.

RUTILUS. Roach: a genus of cyprinoid teleostean fish.

SACCOPHARYNX. Gulper-eel: a deep-sea teleostean fish.

SACCULINA. A cirripede parasitic on the abdomen of crabs, with a free-swimming nauplius larva.

SAGITTA. An arrow-worm: chaetognath, 194

SALAMANDRA. A genus of salamander: urodelan amphibian.

S. MACULOSA. Spotted salamander.

SALMO SALAR. The Atlantic salmon: a teleostean fish.

S. TRUTTA. River or brown trout, 308

SALMONIDÆ. The salmon-trout family of teleosts, with a few deep-sea forms (*Bathylagus*, etc.).

SALPA. A free-swimming, pelagic, transparent tunicate.

SALTICUS. Jumping spider: an arachnid (Araneida, Salticidæ), 214

SANDALOPS. A genus of deep-sea squid: cephalopod mollusc, 203

SAPPHIRINA. A marine planktonic animal: one of the larger copepod crustaceans.

SARCOPHAGA. Flesh-fly: a dipterous insect, 58

SARCOPHILUS. Tasmanian devil: a marsupial (Dasyuridæ), 438

SARCOPTES SCABIEL. The itch-mite: a parasitic mite causing scabies in man (Acarina), 216

SARZIA. Free medusoid form of a hydrozoan cœlenterate, 139

SATURNIA PERNYL. A silk-moth: lepidopterous insect.

SAXICOLA. A genus of passerine bird including the whinchat (thrush family), 417

SCALOPS AQUATICUS. An American, mainly aquatic, mole: an insectivore.

SCAPHIOPUS. American spade-foot toad: an anuran amphibian.

SCAPHIRHYNCHUS. Shovel-nosed sturgeon of North America: a chondrosteian fish.

SCAPHOPODA. A class of molluscs with cylindrical shell, which burrow in the sand—*Dentalium*, etc.

SCELOPORUS. A lizard: lacertilian reptile.

SCHISTOCERCA GREGARIA. Desert locust: an orthopterous insect (Acrididæ).

SCHISTOSOMA HEMATOBIA. The parasitic trematode worm causing bilharzia, 187

SCHIZOPODA. An order of Malacostraca (crustaceans) comprising the opossum shrimps, mysids, etc.

SCIURIDÆ. A family of rodents comprising the squirrels, marmot, prairie-dog, etc.

SCIUROMORPHA. A division of rodents comprising the squirrels, beavers, jumping hares, etc.

SCIURUS VULGARIS. The European red squirrel: a rodent.

SCOLOPENDRA MORSITANS. A centipede: myriapod (Chilopoda), 210

SCOMBRIDÆ. A family of teleostean fish comprising the mackerel, tunny, etc.

SCOPELARCHUS ANALIS. A deep-sea teleostean fish.

SCORPENA. Scorpion-fish: a poisonous teleostean fish, 302

SCUTIGERA. House centipede: a genus of myriapod (Chilopoda), 160

SCYLLIORHINUS CANICULA. European spotted dogfish: a selachian fish, 280

SCYLLIUM. A genus of dogfish: selachian fish.

SCYMNUS. A genus of shark: selachian fish.

SCYPHOZOA. A class of cœlenterates, comprising the jellyfish.

SEDENTARIA. A division of polychæte worms comprising the tube-dwelling (tubicolous) forms, such as *Branchiomma*, in contrast to the Errantia.

SELACHE MAXIMA. The basking shark: a selachian fish, 283

SEMOTILUS. Horned dace of North America: a cyprinoid teleostean fish.

SEPIA. Cuttlefish: a dibranchiate cephalopod mollusc, 201

SEPS. A genus of skink: lacertilian reptile (Scincidæ).

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- TYPHLOPS*. A genus of blind burrowing snake: Typhlopidae.
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- UCA**. Fiddler-crab: decapod crustacean.
- UMBRA**. Mud-fish: fresh-water teleostean (pike family).
- UNGULATA**. Hoofed animals: a former division of mammals, now separated into four orders—Artio- and Perissodactyla, Hyracoidea and Proboscidea.
- URANOSCOPUS*. Stargazer: spiny-rayed marine teleostean fish from tropical seas.
- UROCHORDATA (Tunicata)**. A sub-phylum of marine chordates, comprising fixed and free-swimming forms, such as sea-squirts (Ascidians).
- URODELA (Caudata)**. An order of amphibians, comprising tailed newts and salamanders.
- UROMACER*. A genus of colubrid snake.
- URSIDE**. The bear family of carnivores.
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ZAMENIS. A genus of colubrid snake including the rat-snake of India and the American black snake: Ophidia.

ZENAIIDURA MACROURA. The mourning dove of America, so called because of its plaintive note: Columbidae.

ZENION. Deep-sea teleostean fish (relative of the John Dory).

ZONOSAURUS. Malagasy lizard: lacertilian reptile.

ZONURUS GIGANTEUS. Great girdled lizard of Africa: lacertilian reptile.

ZORAPTERA. An order of minute insects, resembling termites.

ZOSTEROPS JAPONICA. Japanese white-eye: a passerine bird.

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