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 Molluscs 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 (photic, 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.

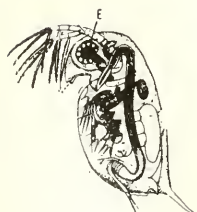Fig. 75.—Richard Hesse (1868–1944).
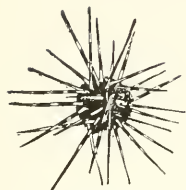
*Diadema
antillarum*

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 remembered [7] 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] *Blatella*—Graber (1883) ; *Periplaneta*—Brecher (1929).
[5] The larvæ of the meal-worm, *Tenebrio*—Tucolesco (1933).
[6] Caterpillars—Lammert (1925), Süffert (1932), Oehmig (1939).
[7] p.

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 duck [2] (Benoit *et al.*, 1952).

Drosophila

Rotifer

[1] p. 537.   [2] p. 559.

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 *Schistostega 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 sentiency 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 ammocœte larva of the lamprey (Parker, 1903–5) and in numerous Amphibians (Nagel, 1896).

Ammocœte 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 vibrissæ so that exploration of the immediate environment is rendered more easy,[2] while the glorified 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 hydrogen atom (von Békésy and Rosenblith, 1951). Similarly, the heat-spots
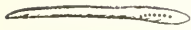
[1] p. 36.
[2] For a general study, see Fitzgerald (1940).

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 undifferentiated[2]; 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.
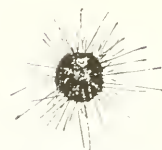
PIGMENTS

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.

Holothuria

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).

Centrostephanus

[1] See further, p. 600   [2] p. 109.

MELANIN

MELANIN ($\mu\acute{\epsilon}\lambda\alpha\varsigma$, 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 chapter [1] they also have a wide integumentary distribution among many species where they may play a dramatic 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 activities [1] (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
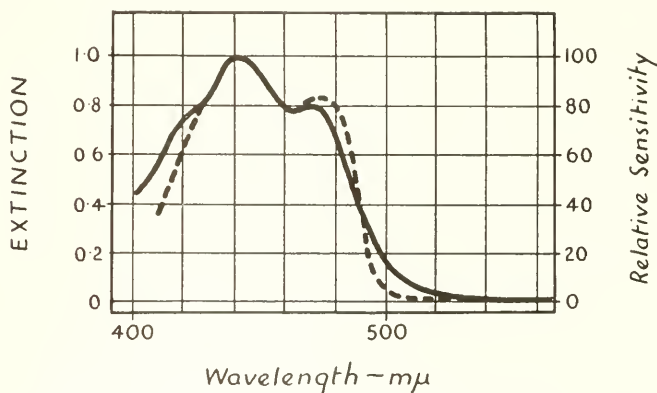
FIG. 77.—SPECTRAL SENSITIVITY OF THE PHOTOTROPIC BENDING OF PLANTS, AND THE ABSORPTION SPECTRA OF THE ASSOCIATED CAROTENOIDS.

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).

(Voerkel, 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 mμ 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 mμ) (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, $C_{40}H_{52}O_4$) (Tischer, 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 Cœlenterates [1] 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
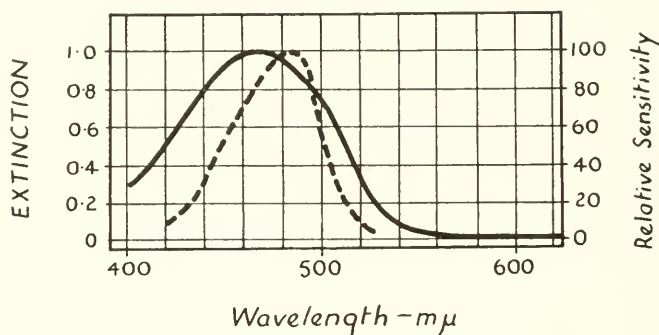
FIG. 78.—SPECTRAL SENSITIVITY FOR PHOTO-ORIENTATION OF THE GREEN FLAGELLATE.

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 retinene$_1$ and vitamin A$_1$ 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] Hybroids of *Sertularia* and *Eudendrium*, maximum absorption 474 mμ, Loeb and Wasteneys (1915).
[2] *Mya*, maximum absorption 490 mμ, *Pholas*, maximum absorption 555 mμ, Hecht (1919).
[3] The earthworm, *Lumbricus terrestris*, and the larvæ of the marine worm, *Arenicola*, maximum absorption 483 mμ, Mast (1917).

Vitamin A_1 has also been isolated in quantity from the eyes of a number of marine Crustaceans,[1] and the occurrence of this photo-chemical 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 A_1 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 found[3]
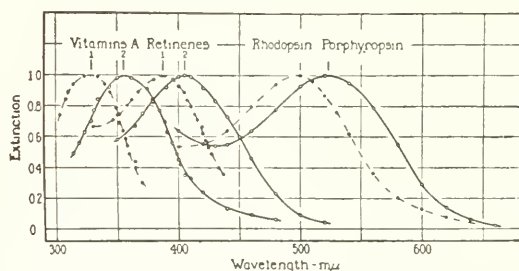
FIG. 79.—SPECTRA OF THE RHODOPSIN AND PORPHYROPSIN SYSTEMS

Direct spectra of crude preparations from the retinæ 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 A_1 system (visual purple) (Steven, 1955) associated with their retinal rods, as also does the majority of marine fishes[4] so far examined ; on the other hand, most fresh-water fishes[5] possess a different system based on vitamin A_2 and retinene$_2$. 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 bergylta* and *Tautoga onitis*), the eyes of which have a pigment based on the vitamin A_2 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 A_2, another probably based on A_1 (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 retinæ 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 retinene$_1$ type with an absorption maximum intermediate between the two main groups (512mμ). Again, the gecko (*Gekko gekko*) has an unusual spectral sensitivity curve, similar to the human scotopic curve but with its maximum displaced 20 to 30mμ towards the red end of the spectrum (Denton, 1956). Retinal extracts from the Australian gecko, *Phyllurus milii*, have shown the presence of an unusual pigment with an absorption maximum at 524mμ, typical of the retinene$_1$ 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 ... es of primates three pigments have been detected: chlorolabe (a green-absorbing p... nt), erythrolabe (red-absorbing), and cyanolabe (blue-absorbing). See Vol. IV, p. ..

[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 (phæommatin). 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 INSECTO-RUBIN, 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.

Augstein. *Klin. Mbl. Augenheilk.*, **50** (1), 1 (1912).

Bayliss, Lythgoe and Tansley. *Proc. roy. Soc. B*, **120**, 95 (1936).

Beadle. *Genetics*, **22**, 587 (1937).

Beadle and Ephrussi. *Genetics*, **21**, 225 (1936).

Becker. *Biol. Zbl.*, **59**, 597 (1939).
Naturwissenschaften, **29**, 237 (1941).

v. Békésy and Rosenblith. *Hb. exp. Psychol.* (Stevens), 1075 (1951).

Benoit, Assenmacher and Manuel. *C. R. Acad. Sci.* (Paris), **235**, 1695 (1952).

Bernard. *Quart. J. micr. Sci.*, **39**, 343 (1897).

Bliss. *J. gen. Physiol.*, **26**, 361 (1943) ; **29**, 277 (1946).
J. biol. Chem., **172**, 165 ; **176**, 563 (1948).

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[1] See Beadle and Ephrussi (1936), Beadle (1937), Ephrussi and Beadle (1937), Mainx (1938), Ephrussi (1942), Ephrussi and Herold (1944), Wald and Allen (1946), Villee (1947), Maas (1948), Okay (1948), Nolte (1954).

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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 cœruleus* 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 ($\sigma\tau i\gamma\mu\alpha$, 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*

Stentor

[1] p. 49.
[2] As occurs in the Algæ, *Cladophora* and *Gonium* (Mast, 1916).

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
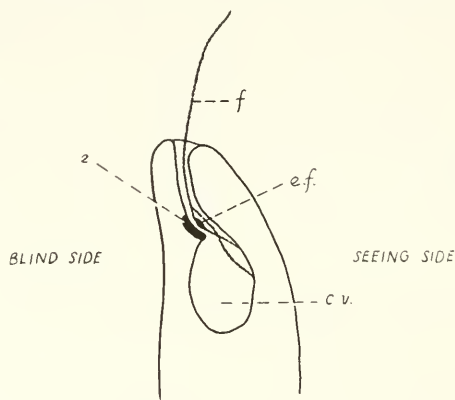reservoir ; it would seem that this is the photoreceptive area and it is

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, astaxan-
thin (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]
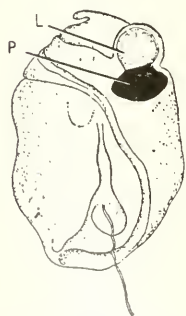
FIG. 81.—THE EYE-
SPOT OF *POUCHETIA.*

Showing the large
pigmented zone, P,
and the lens, 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 pig-
ment 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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Pringsheim, E. G. and O. *New Phytologist*, **51**, 65 (1952).

Schütt. *Ergebn. Plank. exped.* (1896).

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Wager. *J. Linn. Soc. (Zool.) Lond.*, **27**, 463 (1900).

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.

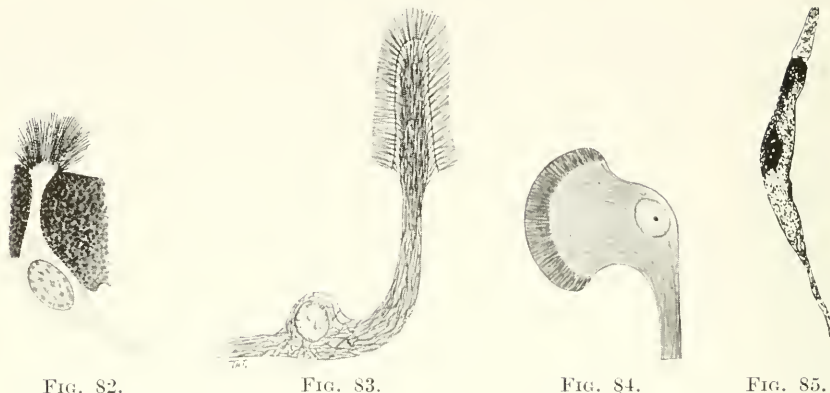FIG. 82.   FIG. 83.   FIG. 84.   FIG. 85.

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,

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 ; OO, optic organelle covered with a denser network of neurofibrils to form the retinella (after W. N. Hess).

that they represent the distal terminations of bundles of the " neuro-fibrillæ " which form the primitive conducting mechanism [2] ; 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.

The second type of receptor is seen among worms and Molluscs ; in it the cell is *apolar* in its general arrangement but contains a light-sensitive mechanism within the cell body (Fig. 86). This typically takes the form of a

[1] p. 243.
[2] See Worley (1933-41).

peculiarly shaped ellipsoidal mass—the OPTIC ORGANELLE (the " Binnen-körper " 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 *Polyophthalmus pictus*, a sedentary Polychæte which abounds in the Bay of Naples (Hesse, 1899– 1908).

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

Leucosolenia

Fig. 87.—Unicellular Eye of the Trematode Worm, *Tristomum papillosum*.

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 sub-epithelial nerve-net sends a nerve-fibre which breaks up into a network of neurofibrils surrounding the ellip-soidal optic organelle [1] ; the sub-epithelial 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 pin-point 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.

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).

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

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 ammocœte larva of the lamprey (Steven, 1951).[1]

Apathy. *Mitt. zool. Stat. Neapel*, **12**, 495 (1897).
Beer. *Wien. klin. Wschr.*, **14**, 255, 285, 314 (1901).
Hess, W. N. *Biol. Bull.*, **38**, 291 (1919). *J. Morph.*, **39**, 515 (1924) ; **41**, 63 (1925).
Hesse, R. *Z. wiss. Zool.*, **58**, 394 (1894) ; **61**, 393 (1896) ; **62**, 671 (1897) ; **63**, 361 (1898) ; **65**, 446 (1899) ; **72**, 565 (1902).
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Kowalski. *La Cellule*, **25**, 291 (1909).
Light. *J. Morph. Physiol.*, **49**, 1 (1930).
Minchin. *Proc. roy. Soc. B*, **60**, 42 (1896).
Steven. *Quart. J. micr. Sci.*, **92**, 233 (1951).
Whitman. *Zool. Jb., Abt. Anat.*, **6**, 616 (1893).
Worley. *Proc. nat. Acad. Sci.*, **19**, 323 (1933).
　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 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*.
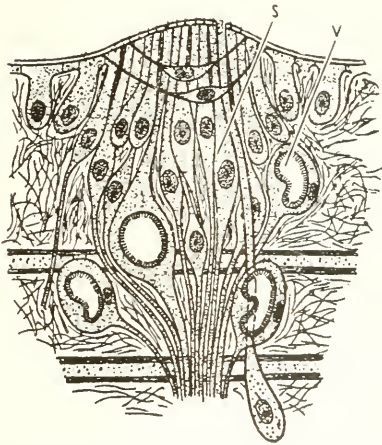
FIG. 89.—The sensory organ of the inter-mediate segments consists of a collection of undifferentiated sensory cells, S, among which are seen the large light-sensitive cells, V (4 in the figure), with the kidney-shaped hyaline optic organelle (after Bütschli).

FIG. 90.—Each " eye " situated in the anterior segments con-sists 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)

Hirudo

[1] p. 131.

Hœmadipsa

(Whitman, 1889–93 ; Maier, 1892 ; Hesse, 1897–1902 ; Bütschli, 1921). In the land-leech, *Hœmadipsa*, the ordinary segmented papillæ 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).
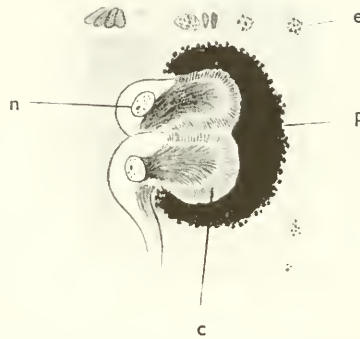
FIG. 91.—The eye of the turbellarian worm, *Planaria torva*, consisting of two light cells with cilia (*c*), nucleus (*n*) and pigment mantle (*p*), the whole lying underneath the epithelium (*e*).

FIG.   —The eye of the turbellarian
   m, *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
Chætognaths, such as the marine arrow-worm, *Spadella* (Hesse, 1902),
and in the median eyes of certain Crustaceans.[1]

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]

Chætognath

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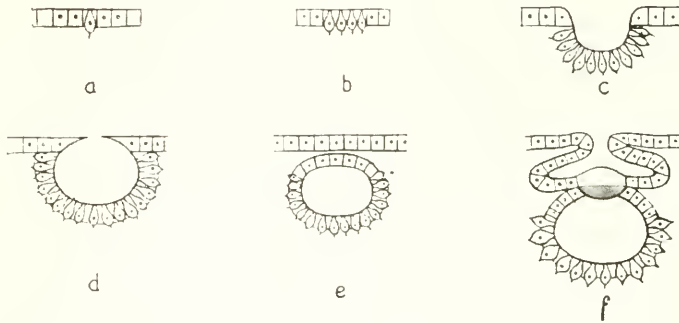
FIG. 94.—SCHEME OF DEVELOPMENT OF THE SIMPLE EPITHELIAL EYE OF
INVERTEBRATES.

    (*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. 94*b*) ; 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.
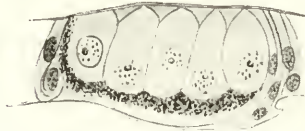
FIG. 95.—The ocellus of the aquatic annelid worm, *Stylaria lacustris* (after Hesse).
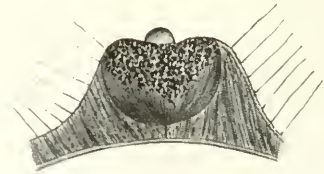
FIG. 96.—The ocellus of the hydro-medusan, *Lizzia*, the epithelial sensory cells being capped by a lens-like thickening of the cuticle (Hertwig and Jourdan).

Dendrocœlum

(Fig. 95) (Hesse, 1908), in certain unsegmented planarian worms such as *Dendrocœlum* 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
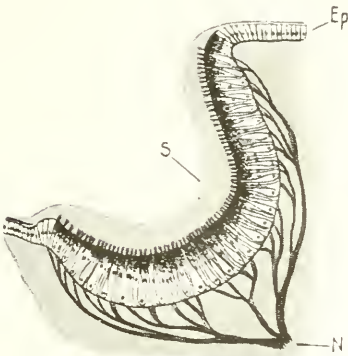
FIGS. 97–100.—TYPICAL CUPULATE EYES OF THE SIMPLEST TYPE.

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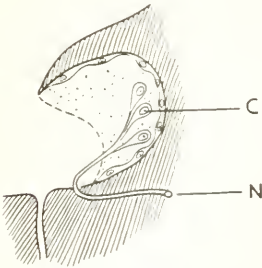
FIG. 99.—The visual organ of the larva of the house-fly, *Musca*.

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).
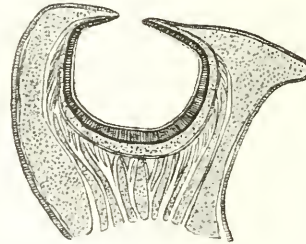
FIG. 100.—The ocellus of the mollusc, *Nautilus*, with its pin-hole opening (after Hesse).
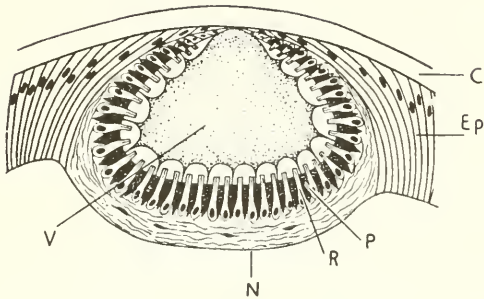
FIG. 101.—The ocellus of the polychæte worm,
Nereis.

C, cuticle ; Ep, epithelium ; N, nerve fibres :
P, pigment between the sensory cells ; R,
nucleated sensory cells provided with cilia ;
V, vitreous (after Hesse).
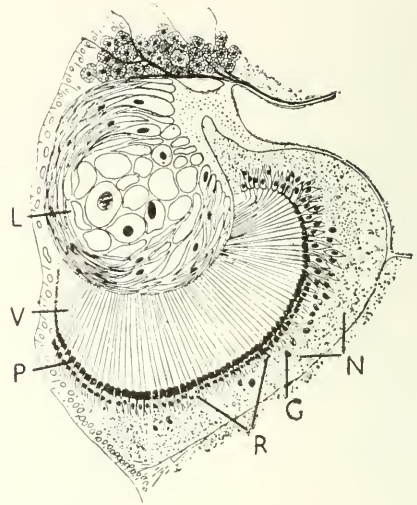
FIG. 102.—The ocellus of the Cubo-
medusan, *Charybdea.*

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).
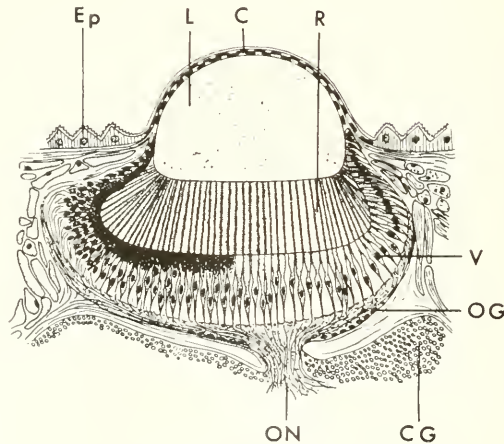
FIG. 103.—The eye of *Peripatus.*

Diagrammatic sagittal section of the eye ; partly depigmented to
demonstrate details of the visual cells.
C, cornea ; 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 ½ 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 polychæte 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

[1] p. 224.   [2] p. 204.

Larva of *Musca*

Nautilus
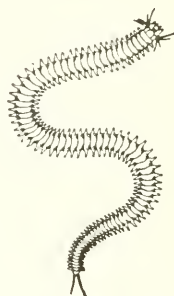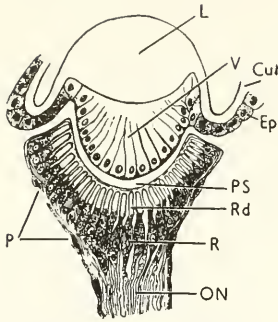

Nereis

Sarsia

Pediculus

Peripatus

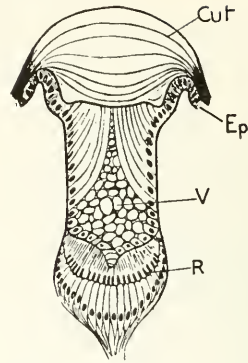FIG. 104.—The frontal stemma of the imago of the blow-fly, *Calliphora* (after Lowne).

FIG. 105.—Sagittal section of the median anterior ocellus of the jumping spider, *Salticus* (after Büt-schli).
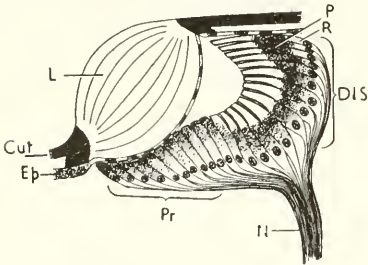
FIG. 106.—The frontal ocellus of the hover-fly, *Helophilus*.

DIS, cells with long sensory ends lying distant from the lens ; Pr, cells with short sensory ends lying proximally to the lens (after Hesse).
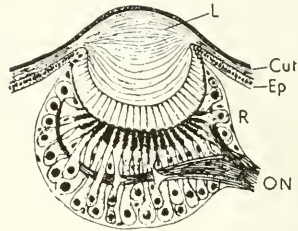
FIG. 107.—The anterior median ocellus of the house spider, *Tegenaria domestica*.

It is to be noted that the optic nerve fibres, ON, issue from the lateral aspect of the visual cells, R (compare p. 159).
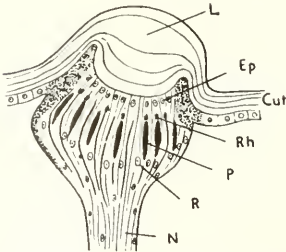
FIG. 108.—The dorsal ocellus of the insect, *Aphrophora spumaria* (after Link).

In Figs. 108–9 the eye is in every sense simple although there is some association of the visual cells around rhabdomes,
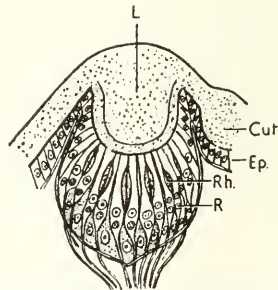
FIG. 109.—The lateral ocellus of the scorpion (after Lankester and Bourne).

Cut, cuticle ; Ep, hypodermal epithelium ; L, cuticular lens ; N, ON, optic nerve fibres ; P, pigment cells ; PS, preretinal space ; R, retinal (visual) cells ; Rd, rods or rhabdites ; Rh, rhabdomes ; 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 (Ten-
thredinidæ) 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 ($\dot{\rho}\alpha\beta\delta\omega\mu\alpha$,
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).

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 mesen-
chyme. In its simplest form such an eye is merely a spherical vesicle
lined with ectodermal cells ; the cells of the proximal (deep) part of
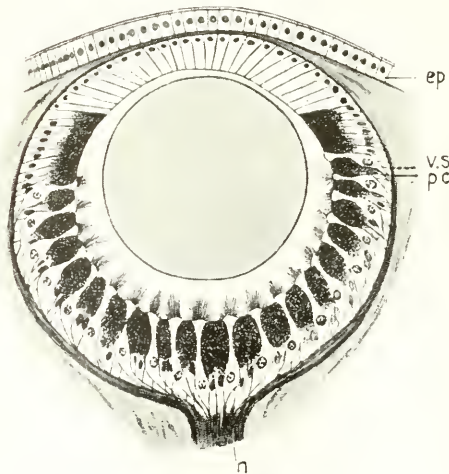

Helophilus

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. Prince).

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.

Shell of
Pterocera

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 Polychætes in the family of Alciopidæ, 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 Alciopidæ, a family of pelagic polychætes (*Alciopa*, *Vanadis*, etc.), have received considerable study [1] (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 mechanism [2] and the eyes are moved by 3 extrinsic muscles. Nothing is known about the function of these elaborate eyes.
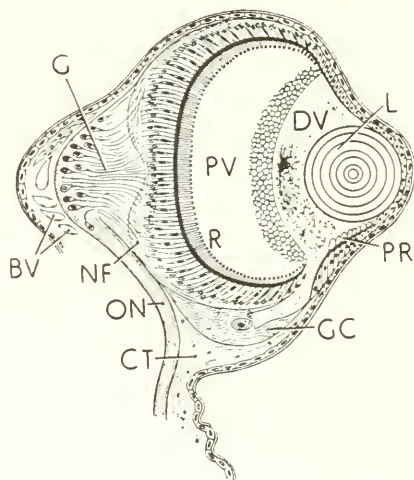
FIG. 112.—THE EYE OF THE POLYCHÆTE WORM, *VANADIS*.

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), Krohn (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.

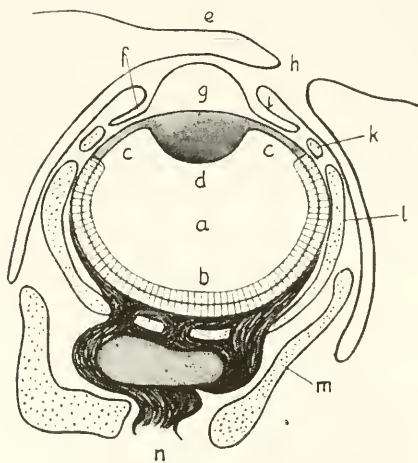FIGS. 113 AND 114.—THE EYE OF A TYPICAL CEPHALOPOD.

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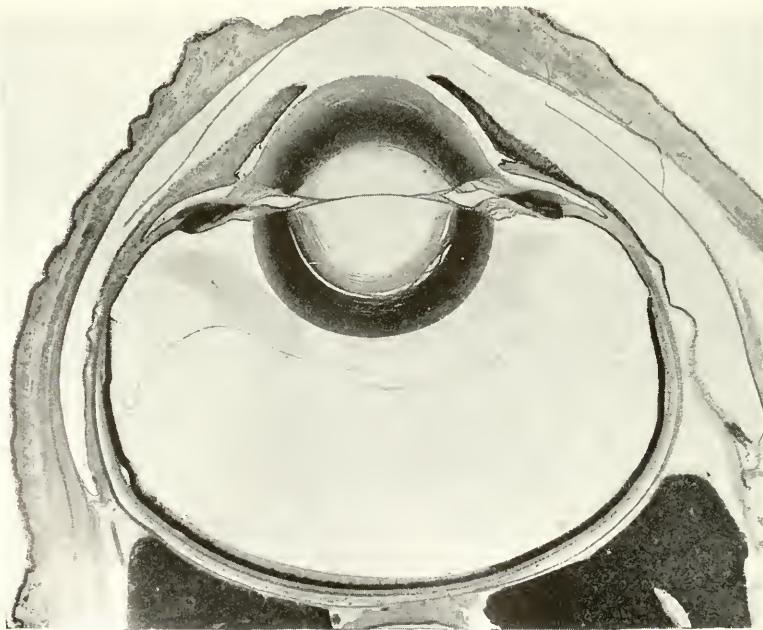
FIG. 114.—The eye of *Octopus vulgaris* (specimen from J. Z. Young).

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*), some-
times, in Œgopsidæ, 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 rect-
angular in shape and actively contractile and there is an efficient accommodative
mechanism [1] (v. Hess, 1909) ; while covering the iris and extending some distance

Sepia
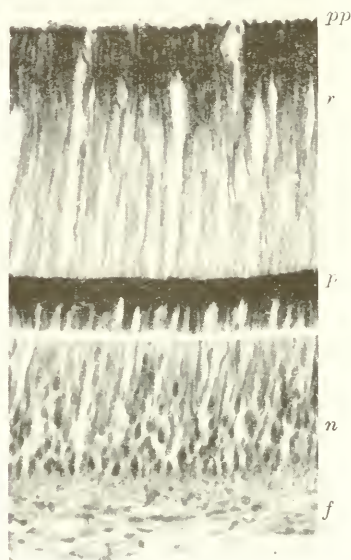
FIG. 115.—THE RETINA OF THE OCTOPUS.

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).

Loligo

Octopus

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

[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
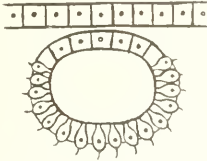

FIG. 118.—THE VERTED RETINA OF
THE VESICULAR EYE.
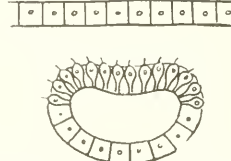
FIG. 119.—THE INVERTED RETINA OF
THE VESICULAR EYE.
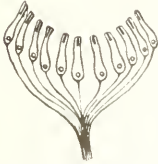
FIG. 120.—THE ARRANGEMENT OF THE
VISUAL CELLS IN THE VERTED
RETINA.

FIG. 121.—THE SIMPLEST ARRANGE-
MENT 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
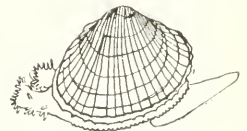
Cardium

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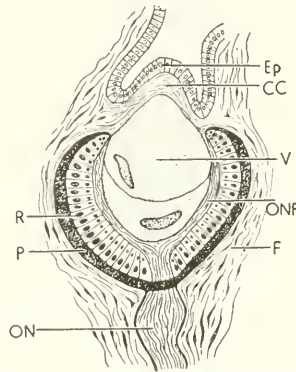
FIG. 122.—The dorsal eye of *Onchidium*.
Showing an inverted retina pierced by the fibres of the optic nerve, resembling the arrangement in Vertebrates.

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).
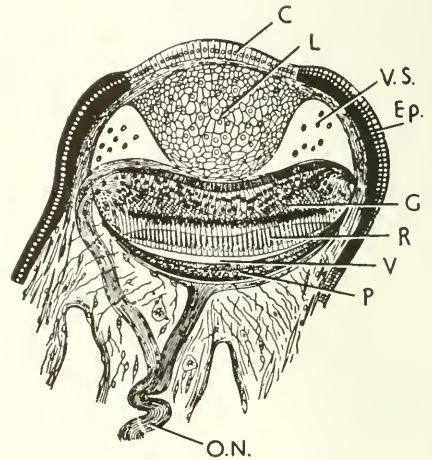
FIG. 123.—The eye of *Pecten*.

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,

e Keferstein (1862), Patten (1886), Kalide (1888), Carrière (1889), Schreiner (189 esse (1900–2).
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

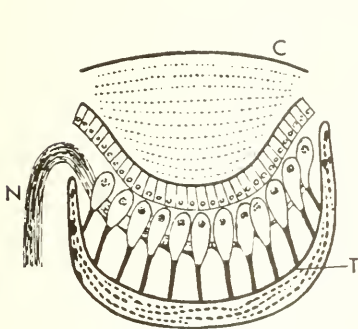FIGS. 124 TO 127.—INVERTED AND SEMI-INVERTED RETINÆ in ARACHNIDS.

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

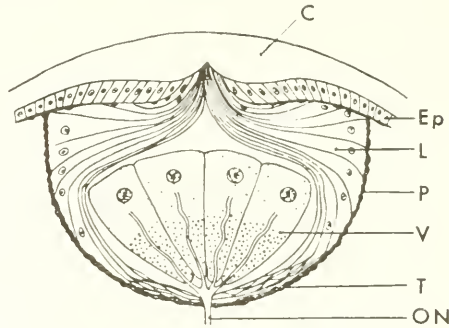C, cuticular lens ; N, optic nerve fibres ; T, tapetum (after Versluys and Demoll).

FIG. 125.—The eye of a sea-spider.

C, cuticle ; 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).
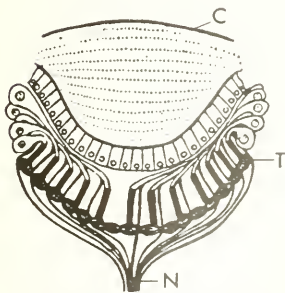

FIG. 126.—The lateral eye of a spider.

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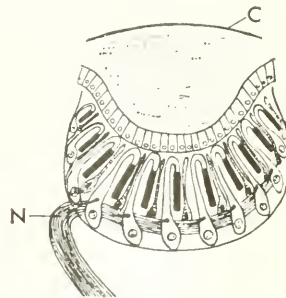

FIG. 127.—The median eye of a whip-tailed scorpion.

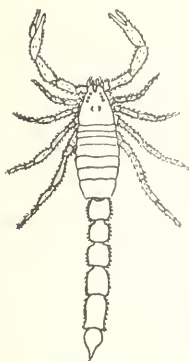C, cuticular lens ; N, optic nerve fibres (after Versluys and Demoll).

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 retinæ (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 planarian and nemertine worms [2] wherein the visual cells dip downwards from

organ (1891), Korschelt and Heider (1893), Bouvier (1913), Wiren (1918), Sch   (1933).
[2]   134.

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.
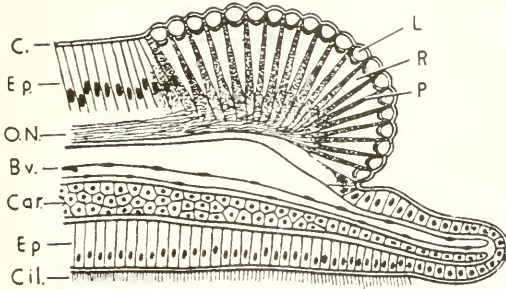

Stylops

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

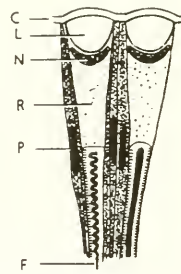FIG. 128.—Cross-section through a branchial filament of the worm.

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 lamellibranch 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 lamellibranch molluscs, *Arca* and *Pectunculus* (Carrière, 1885 ; Patten, 1886 ; Hesse, 1900).
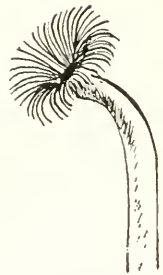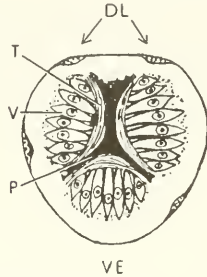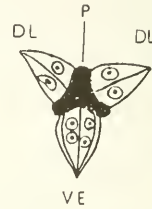

Branchiomma

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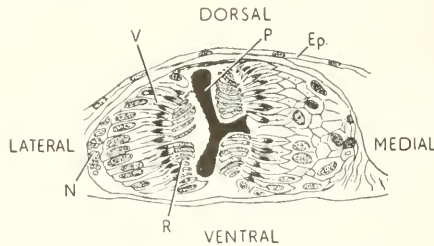
FIG. 132.—The ocellus of the chætognath, *Spadella exaptera*.

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 (Chætognatha), *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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Jch. 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
(1801–185.), (Fig. 133), Professor of Physiology first at Bonn and then at Berlin,
a student friend and collaborator of von Helmholtz. In association with
Malpighi   Haller, he may be considered the founder of the great German
School of   iology 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 physiology [2] 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
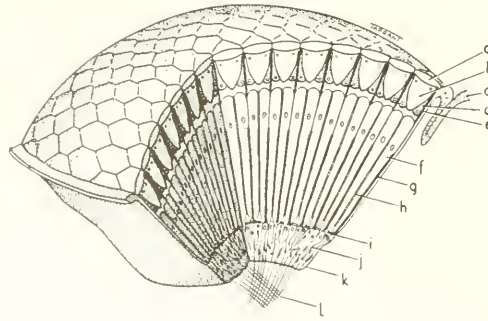

FIG. 134.—THE COMPOUND EYE.

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 (ὄμμα,

[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. ὀμματίδιον) ; 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 ;
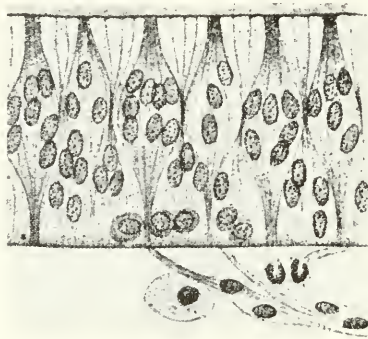

FIG. 135.—THE DEVELOPMENT OF THE COMPOUND EYE.

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 Watase (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 ommatidial eye 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 polychæte 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
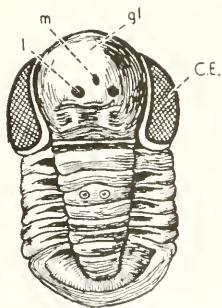

FIG. 136.—RECONSTRUCTION OF THE
FOSSIL TRILOBITE, *ÆGLINA PRISCA*.

On the glabella (*gl*) there are impressions of a median, *m*, and paired lateral ocelli, *l*. The compound eyes, CE, are very large (after Barrande).
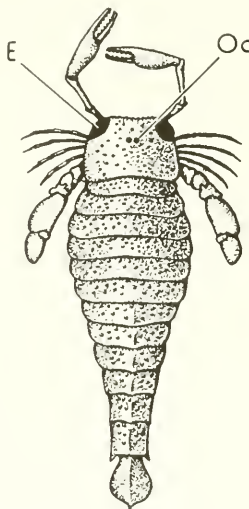
FIG. 137.—RECONSTRUCTION OF THE
FOSSIL EURYPTERID, *PTERYGOTUS ANGLICUS*.

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
retinular 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 retinular cells are the photosensitive elements [1]; 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 retinular 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 retinular 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.

retinular 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
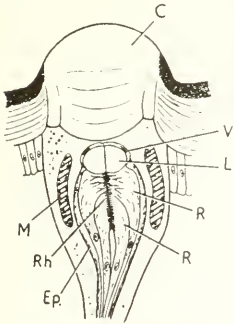

FIG. 138.—THE SIMPLE OMMATIDIAL EYE OF THE LARVA OF THE MOTH, *GASTROPACHA RUBI.*

A lens and retinule are arranged after the manner of a single ommatidium (after Demoll).
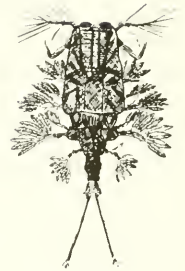
C, corneal lens ; Ep, epithelial cell ; L, lens ; M, mantle cell ; R, R, visual cells ; Rh, rhabdome ; V, vitrellæ.

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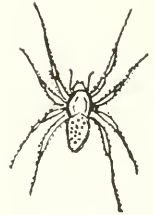p between an ocellus and an ommatidium. Thus the female *Pontellopsis regalis,* for example, has an eye composed of a single retinule of 6 cells arranged in two groups of 3 (Vaissière, 1954), while *Copilia* and its relatives have a single group of 3 cells arranged around a rhabdome (Grenacher, 1879–80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

Copilia

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).

Tegenaria

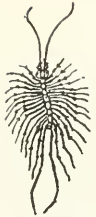True compound eyes, however, are seen only among the Arthropods. They occur in several fossil forms (Trilobites, Eurypterids,

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 is 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 (Cerambycidæ) (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 organ [1] (*Stylocheiron mastigophorum*—Chun, 1896) (Fig. 141).
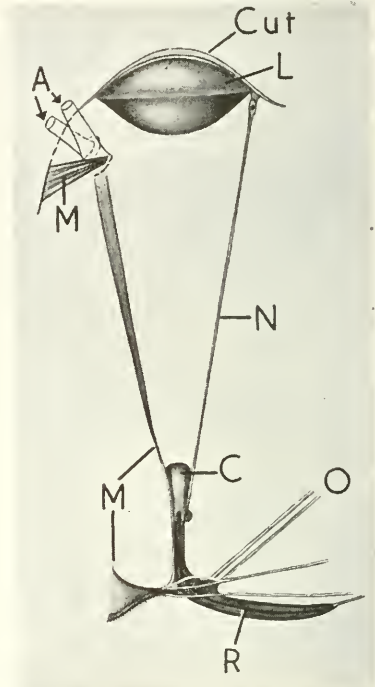
Scutigera

Phronima

Dineutus

Stylocheiron

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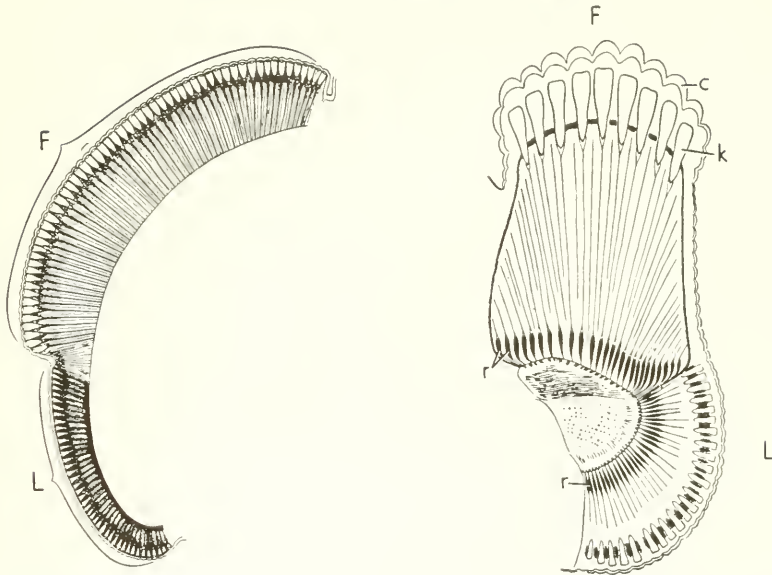
FIG. 140.—Frontal section of the eye of the male April fly, *Bibio marci*.

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

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

F, frontal eye ; L, lateral eye ; c, corneal lens ; k, crystalline cone ; r, rhabdomes. 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 obscure [1] (Fig. 143).

Limulus

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
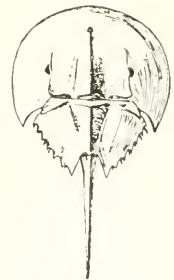
[1] See Lankester and Bourne (1883), Watase (1890), Miller (1952), Waterman and Wiersma (1954).
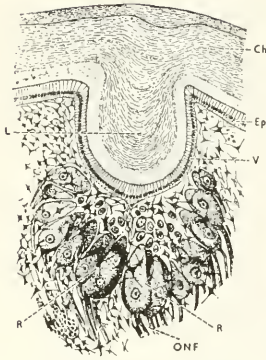
FIGS. 142 TO 144.—THE EYES OF THE KING-CRAB, *LIMULUS POLYPHEMUS.*
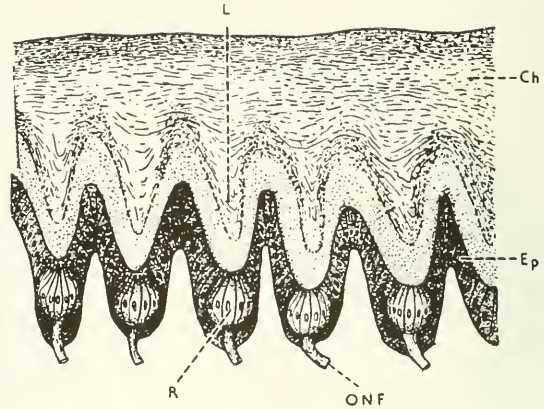
FIG. 142.—The median eye.

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).
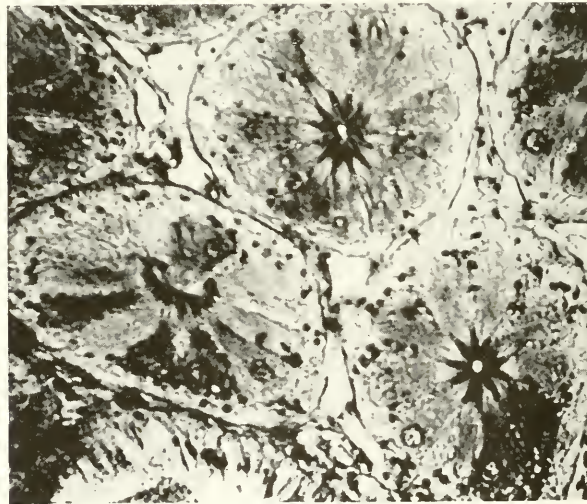
FIG. 144.—Section of the lateral eye.

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 (Cypridinae, etc.).

Leptodora

Polyphemus

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 exist [1]; 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
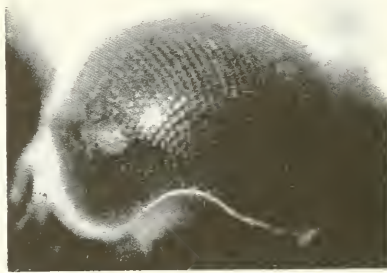

Fig. 146.—The Eye of a Crayfish.
Showing the faceted appearance of the compound eye (Norman Ashton).

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 (1909), Wenke (1908), Hesse (1908), Strauss (1909), Demoll (1909–17), Doflein (1914), Bernards (1916), Herter (1928), Fricke (1931), Hanström (1931–35), Welsh (1937), Hekly and Kupka (1942).
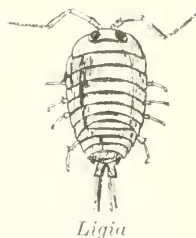
short outer. a main intermediate. and a hollow inner segment. The
retinule consists of relatively few cells (4 in crabs) grouped around the
central rhabdome. the proximal extremity of which rests on a fenes-
trated membrane. There is evidence that the retinular cells are not all
of the same kind ; thus 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.

Ligia

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 them-
selves also contain melanin ; while at the level
of the retinule is a clear reflecting pigment [1]
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 sur-
rounding the retinal elements. cleared of absorb-
ing pigment, act as a functional *tapetum*. We
have already seen that the migration of these
pigments often shows an autochthonous diurnal
rhythm [2] and that. in addition to this response

FIG. 148.—THE OMMATI-
DIUM OF THE CRAY-
FISH, *ASTACUS*.

On the left, in the light-
adapted, and on the right.
the dark-adapted state.

a, Cornea ; b, hypo-
dermal corneal cells ; c,
body of crystalline cone ;
d, inner segment of crys-
talline cone ; e, retinal
pigment cells ; f, rhab-
dome separating retinular
cells ; g, tapetal cells ; h,
basement membrane (mo-
dified from Bernhards).

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).

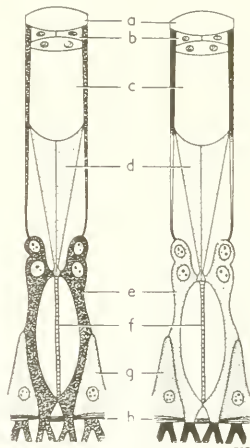[2] p. 19.   [3] See further p. 554.

Lobster

We shall see [1] 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 eye [2] adapted for dim illumination (Edwards and Bouvier, 1892).

Prawn

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,
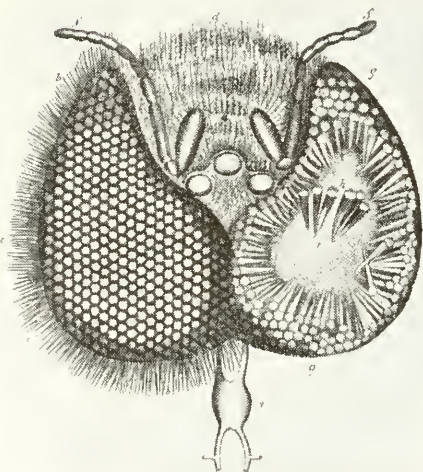

Fig. 149.—The Eyes of Insects.

An old anatomical drawing from Swammerdam (*Bybel der Natuure*, 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).
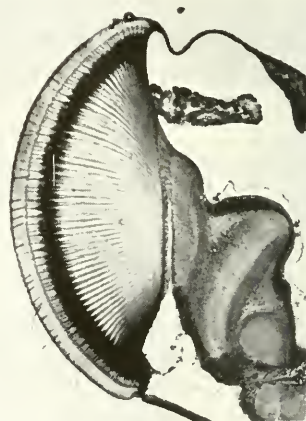
Fig. 150.—The Compound Eye of the Bee.

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 (1911), Bedau (1911), Geyer (1912), Demoll (1912–17), Zimmermann (1913), Jörschke (1914), Gugnion 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 EUCONE 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.
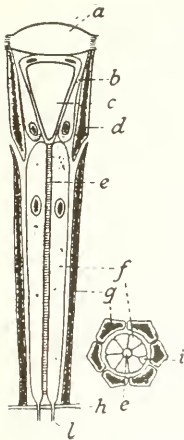

FIG. 151.—The apposition eye, with (alongside and below) a section through the retinule.
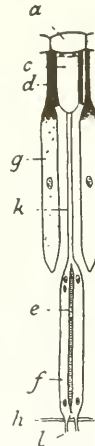
FIG. 152.—The superposition eye in the dark-adapted condition with the pigment in the iris cells almost entirely withdrawn into their upper extremities.

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 (*vitrellæ*), 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-refringent (the ACONE EYE). Alternatively, the refractive

(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), Ehnbom (1948), Tuurala (1954), Fernández-Moran (1956).

Crane-fly
(Tipulidæ)

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
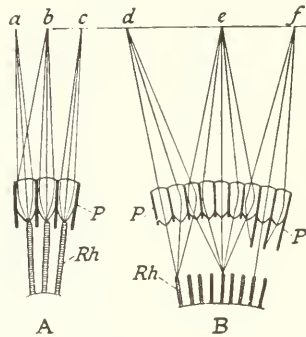

FIG. 153.—IMAGE FORMATION IN THE COMPOUND EYE.

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 acts optically as an isolated unit.   The iris cells contain not only blue-absorbing pigment but also pale or coloured reflecting granules with 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, *Lampyris*. 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.

Fire-fly

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

[1] p. 173.

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 super-position 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.

Butterfly
(*Vanessa*)

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).

Notonecta

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 contradistinction to 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, *Lampyris*, 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
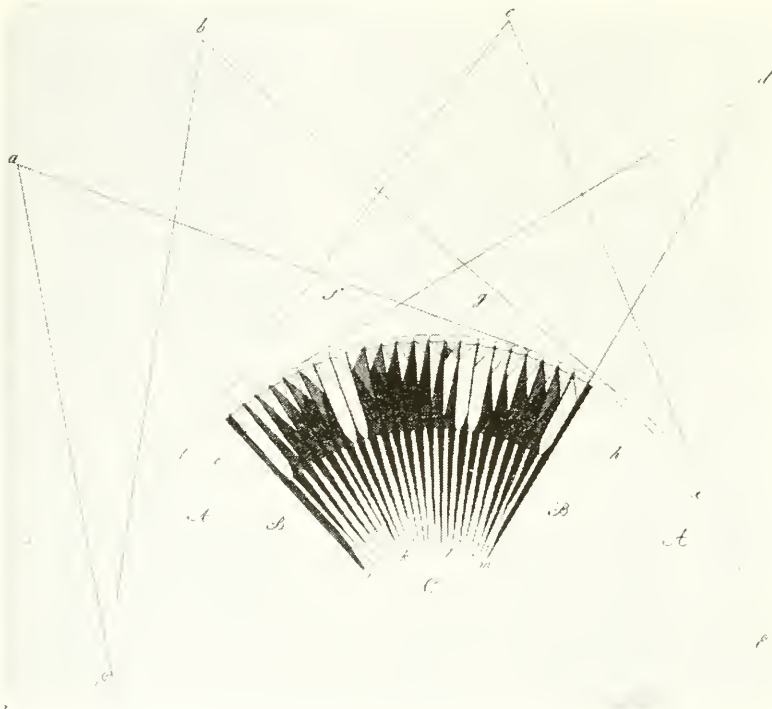

FIG. 156.—THE COMPOUND EYE ACCORDING TO JOHANNES MÜLLER.

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 40μ) ; 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
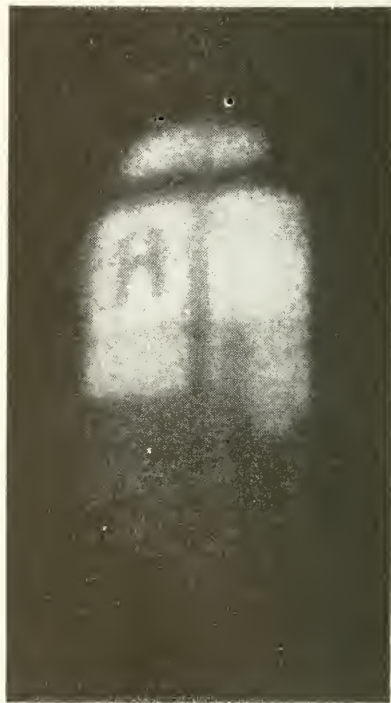

FIG. 157.—EXNER'S CLASSICAL PHOTO-GRAPH THROUGH THE OPTICAL SYS-TEM OF THE COMPOUND EYE OF *LAMPYRIS SPLENDIDULA*.

Showing a window with a letter R on one pane and a church beyond (from Wigglesworth's *Principles of Insect Physiology*, Methuen).

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° (Burtt 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 (Autrum 1949) (Fig. 158).

Exner's early work on the dioptrics 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 lamellæ 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
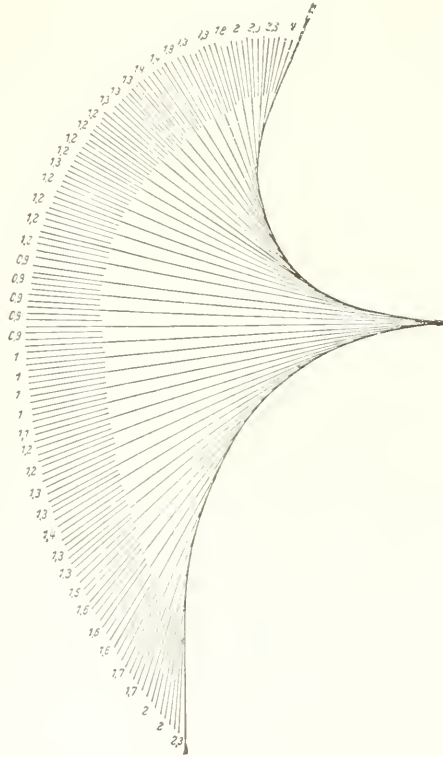
Forficula

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 wavelengths 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
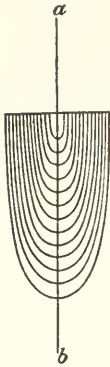
Locusta

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
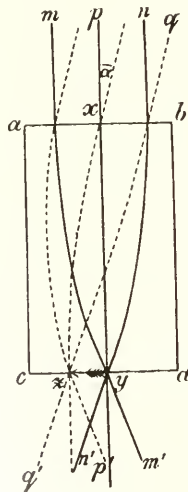

FIG. 160. —THE OPTICAL SYSTEM OF THE APPOSITION EYE.

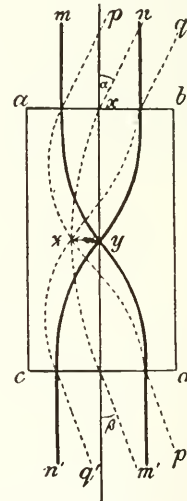The lens cylinder is equal in length to its focal distance (after Exner).

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 retinular cells act as differentially orientated detectors[1] 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 transmission[2] ; 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 ultrastructure 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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