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An Introduction to the Behaviour of Invertebrates

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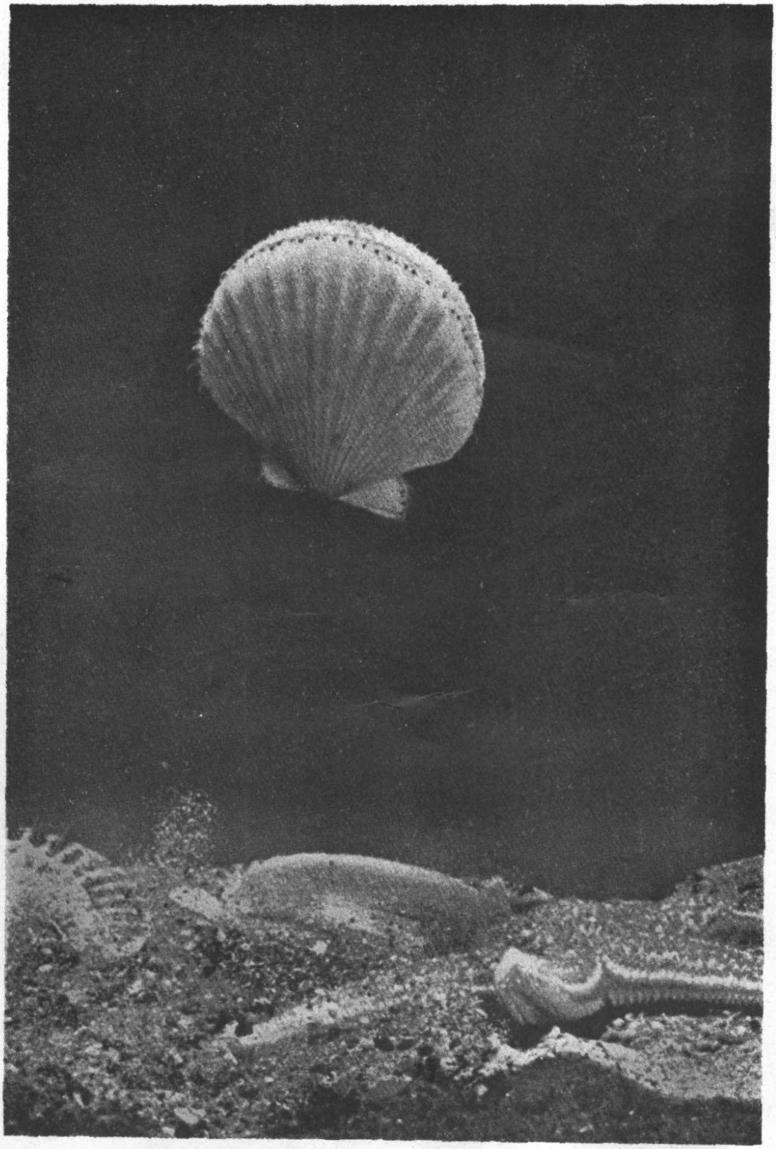

FRONTISPIECE. A queen (*Chlamys opercularis*) swims upward at the approach of a starfish (*Asterias rubens*). Note the sensory tentacles and the eyes along the mantle edge of this close relative of the scallop (*Pecten* sp.).

(*Photo: D. P. Wilson*)

PREFACE

WHILE preparing this book, it has become obvious that greater attention has been paid to the behaviour and sensory physiology of insects than to the rest of the invertebrates. An attempt has therefore been made to strike a balance and as far as possible to draw conclusions which may be applicable throughout the invertebrate subkingdom—though the very diversity of those animals militates against this. The mass of work still waiting to be done on invertebrates other than insects stands accentuated once again.

I have not been concerned here with the pros and cons of terminology, such as the implications of the terms taxes and kineses, but have used the few which do appear as names for observational concepts without inferring anything more, nor, indeed, implying physiological or anatomical mechanisms, unless they have been discussed specifically.

The debt which this book must owe to its predecessors in this field is great and the help I have derived from Warden, Jenkins and Warner's *Comparative Psychology*, Fraenkel and Gunn's *Orientation of Animals* and W. von Buddenbrock's *Vergleichende Physiologie*, was invaluable, not least in introducing me to work which I had not encountered already.

It is always difficult for a non-systematist to be certain that the specific names he is using are the correct ones. With the help of various members of the staff of the British Museum of Natural History, I have brought the specific names up-to-date so far as possible. After the first mention, an animal is always referred to by its modern name though this may differ from that used in the original paper.

In the search for the literature many librarians have given me willing aid, but most particularly I have persistently troubled the Librarians and their staffs of Queen Mary College and the Zoological Society of London, never failing to get help and advice from them.

Several people have given their time to reading parts or all of this book and I hope I have met their criticisms. Of these persons, I would like to express my very grateful thanks to G. E. Newell, C. F. A. Pantin and J. E. Smith, without, in any way, wishing to suggest that they can be held responsible for any of the inadequacies of this book.

My wife gave me much practical help, as well as encouragement, when needed. Miss J. Hawkes aided in some of the final typing and the indices were prepared most efficiently by G. J. Peakin. A

number of drawings were made by W. Tschernezky; their clarity speaks for itself.

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CHAPTER I

INTRODUCTORY

THE behaviour of an animal is the result of information fed into the co-ordination system, nervous or otherwise, relating to two sources, one, the external conditions of the environment, and the second, the state of the individual itself. Since the form of the information is the stimulus received at a sense organ—where these exist—it has become customary to consider the sense organs as exteroceptors and interoceptors. However, this is an artificial distinction since no sense organ receiving stimuli from outside can escape the influence of the internal, physiological state of the body.

Nor is the pattern resulting from these stimuli determined solely by them but is strongly influenced by this same internal state—whether the animal is hungry or replete, old or young, in reproductive condition or not, to take examples. Also there may be rhythmic activity patterns inherent, and even innate, in the central nervous system, which influence the expression of the sensory inflow as motor action.

We shall be mainly concerned in this book with the behaviour of invertebrates in response to external factors and the role which this behaviour plays in the natural life of the animal. These factors which characterize the external environment may be arbitrarily divided into chemical and physical ones. From this arises the division of sense organs into mechanoreceptors, receiving physical stimuli such as pressure, radioreceptors, receiving stimuli in the form of radiant energy, that is light and heat, and, finally, chemoreceptors stimulated by chemicals. Both classifications are matters of convenience and cannot be rigidly applied especially when it is not clear what sense is involved. Thus, humidity differences could be detected either by their effect on chemoreceptors or by changes in the physical properties of structures, these affecting mechanoreceptors. It is characteristic of all stimuli that they are forms of energy which can be transferred across a sensory cell surface and passed along a nerve as a series of electrical and chemical changes.

In general, the physical factors are those of light, heat, gravity, pressure. To these might be added electricity but since there is no evidence at the moment that invertebrates require to react to this stimulus under natural conditions, and indeed probably rarely encounter conditions in which the stimulus is important outside the laboratory, this will not be dealt with in this volume. But it must be admitted that the evidence of electrical sensitivity in the mormyrid fishes[336] makes it advisable not to be dogmatic concerning the unimportance of electric fields as stimuli in nature.

Different sense organs may react to different qualities of a single source of stimulation. Thus, animals may react to the wavelength characteristics of light, called by us, colour, or to the plane of the wave movement, as polarized light, or simply as a straight beam from the direction of movement of the constituent waves.

Both physical and chemical stimuli arise from living and from inanimate sources. All act as indicators of the state of the environment and thus of the ecological conditions in which the animal finds itself. Behaviour plays an important part in maintaining an animal in its optimum ecological environment. Obviously, indeed, as this is one essential for survival of the species, even if it is not necessarily so for the mere existence of the individual.

It may be true to say that the simpler the animal's requirements the simpler its responses, while the wider the range of conditions which it can tolerate the more complex become its responses, enabling it to make the fine adjustments necessary for existence in the different parts of its survival range. The behavioural responses of invertebrate animals to their surroundings are often very simple, consisting solely of random movement under particular stimulation (kineses) or of movement directed with respect to the source of stimulation (taxes). Simplicity of responses in these cases may be indicated by attention to one factor, or source of stimulation, at a time without evidence of choice of this factor. Choice, and its frequent accompaniment, the ability to learn, are not absent from the behaviour of invertebrates, most of whom possess these abilities to some degree, while they rise to a height among the cephalopods and among the social insects, where they appear to be accompanied by a process of abstraction and symbolization in the dances of honeybees superior to that of any other invertebrates.

Simplicity and rigidity of response is often coupled with simplicity of central nervous organization. The simple nerve net of coelenterates may form through-conduction tracts, as they do in the Actinozoa, but the greater part of the system retains its diffuse arrangement. It may be said that the more diffuse the nervous system the more stereotyped the response, for parts tend to be autonomous, depending upon local reflex arcs. Without central control variability of reaction may be reduced. Bi-lateral symmetry and anterior-posterior polarization of the body bring with them condensation of the nerve cells along the axis of the body with the formation of a nerve cord and brain. By a process of cephalization the sense organs become collected at the anterior end; with this end leading in movement this arrangement is functionally more efficient, in that food detecting and food collecting organs, for example, are often drawn together into the most advantageous position. The concentration of sense organs produces enlargement of that end of the central nervous system to form a brain. Its function is essentially to correlate the sensory inflow from the sense organs and on this information to channel the nervous activity into the appropriate motor outflows. Further increase in the relative size of the brain produces more complex and more variable behaviour, due to the great increase in the number of internuncial neurones enlarging the possible interconnections that can be made.

Behaviour is attuned to the normal conditions of the animal's life, that is, the conditions which occur with the greatest frequency in nature. Further, normal behaviour is apparently purposive because it has survival value or one supposes it would not achieve the level of development that the normal patterns do reach in the average animal. It is under the extraordinary conditions of an experiment, or under some unusual turn of events, that the behaviour, particularly that of the rigid, instinctive type, may appear to be useless or even directly fatal to the animal. These are important considerations when evaluating the results of experiments on the effects of different factors.

Since a major limiting factor on reaction to a particular stimulus is the ability of the sense organs to receive the stimulus, many behaviour experiments are, in fact, evaluations of the sensory abilities of the animals concerned. It is therefore appropriate to consider sense organs in general terms at the outset.

CHAPTER II

THE SENSE ORGANS

MOST behaviour is initiated by the reception of stimuli by some sense organ or another. Indeed sense organs, being responsible for receiving and measuring the characteristics of the surroundings, are the means by which the animal keeps, often literally, in touch with the outside world. The extent of their ability to carry out this task imposes a limit on the range of an animal's behaviour. The essential parts of them all are the sensory cells which act as transducers translating the energy form of the stimulus, chemical or physical, into nervous energy by a variety of paths. The ancillary apparatus of the simpler sense organs serves to increase the efficiency of this process by concentrating the stimulus on to the sensory surface. The temporal pattern of the stimulus can alone be perceived through such an organ but more complex ancillary apparatus may make the spatial pattern of the stimulus perceptible. Thus a light sensitive cell in the skin of an earthworm may react to consecutive light and dark, but a retina and the addition of focusing apparatus is required for the perception of images formed by the simultaneous presentation of light and dark patches (there is evidence, however, that image perception depends upon a temporal patterning of the stimulus, so that the details of an object cannot be perceived unless either the moving eye scans it or it moves itself when its details can be perceived through a stationary eye [586a]).

The impulses passing from the sense organs make their appearance on experimental apparatus as electrical impulses, accompanied by shifts of chemical substances which may be the result, or the cause, of the electrical changes. Conduction of excitation along nerves seems to depend upon these electrical effects. Thus the integration of the body into a functional whole by its nervous system will also depend upon electrical phenomena of this sort.

In this conversion the form of the information is also altered. The wave form of the light received by an eye is not reflected in the wave form of the electrical impulse passing down the nerve. Instead, if the nerve reacts at all, it reacts at maximum intensity (the all-or-nothing law) but with a frequency that is directly proportional to the strength of the stimulus, though as a result of adaptation this frequency may decrease with continued stimulation at the same strength. Thus reaction to light is indicated in the optic nerve by pulses of electrical energy rising to a fixed level; as the light is increased in brilliance, so the frequency of the pulses increases though the height of each pulse remains the same. In this way not only is the information that a particular source of stimuli is in the animal's vicinity conveyed to the central nervous system but also the strength of the stimuli emanating from it is measured.

The sensitivity of the receptor cells varies very greatly. A chain of impulses will not leave the cell until the stimulation reaches a definite value, the threshold, which is fixed for that particular type of cell in that particular species of animal at the time of measurement. Two cells reacting to the same stimulus in two animals of different species will not necessarily have the same threshold and changes of the physiological state of an animal may alter the thresholds of its nerve cells. Once the information has reached the central nervous system the reaction to it is not fixed. The motor directions which leave the central nervous system will be affected by the other sensory impulses arriving in the motor centres and also by the physiological state of the animal. For example, the reactions of a fully satisfied blood-sucking tick are different from those of a hungry tick seeking a blood meal and the reactions of a planarian worm to currents depend upon whether it is about to lay eggs, or has already done so.

Though it may be clear from the behaviour of an animal that it is receiving certain forms of stimulation, it may not always be possible to single out any structures as those responsible for perceiving the stimuli. Many insects retain a limited ability to behave towards light stimuli even after their eyes and ocelli have been blackened. The sensory apparatus for such behaviour has not been demonstrated. However, in general, there is good information about the structure of the sense organs responsible for the various reactions though the morphology of them is so varied in detail that it is impossible to give more than a general review here.

LIGHT RECEPTORS

The ability to react to light usually depends upon the existence of definite organs or, in the case of non-cellular animals, organelles. These receptors may be simply for the perception of the direction of light, like the ocelli of insects, or light sensitive cells in the epidermis of earthworms, in which case they can be termed 'euthoscopic'[420] eyes. There is usually some structure masking the sensitive cells so that light is perceived from one direction only, and a lens may be developed to concentrate the light upon sensitive cells. But the receptor has to become a more complex eye, when the pattern of light is to be perceived, that is, when images are perceived. This is an 'eidoscopic' eye. This requires some method of moving the lens relative to the screen, in other words, a focusing device by which the shape of the lens can be altered, changing its focal length, so that a clear image falls upon the screen, which must be capable of resolving it.

The receptors may be unicellular or multicellular. The complex organization of the protozoan body may culminate in the complex specialization of parts for a variety of functions. As a result sense organelles are developed which are sensitive to light. One of the

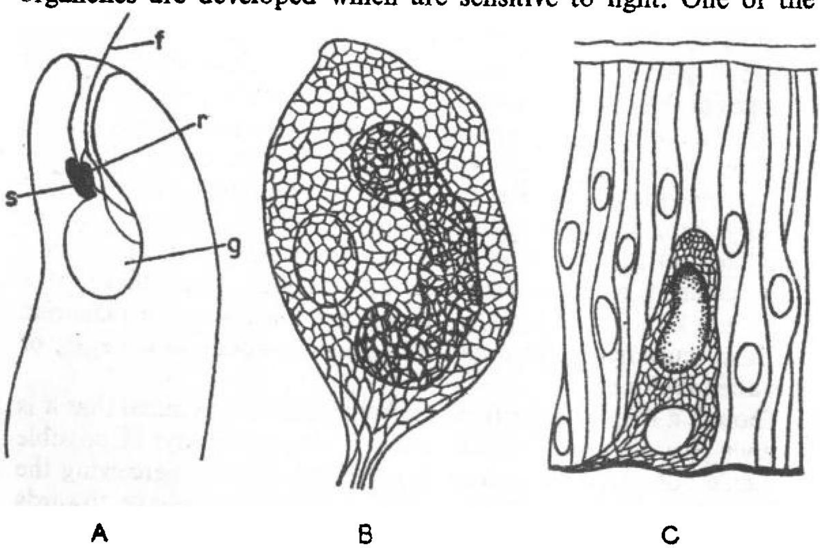


FIG. 1. Light receptors. A. Gullet and base of flagellum of pigment spot; r, receptive area; f, flagellum; g, gullet (after Mast[368]) B, Light sensitive cell from epidermis of earthworm. And C, part of the epidermis showing a sensitive cell in position. (after Hesse[263])

simpler of these is found in *Euglena*. Here the sensitive spot is a hyaline enlargement near the base of the flagellum. This is shaded from one side by a yellowish-red cup lying in the cytoplasm (Fig. 1A), thus producing the masking essential in a light receptor which is to be used to obtain direction from light rays. The organelle may become more complex as in the dinoflagellate *Pouchetia*, whose amoeboid pigment spot is surmounted by a sphaerulitic lens, with, it is supposed, a light sensitive area lying between the two; the two considerations of masking for localization of the direction of the light and of concentration by means of a lens are fulfilled.

An example of single cells specialized for light reception are the photo-receptor cells scattered over the epidermis of the earthworm.

Each of these contains a hyaline lens which appears to concentrate light upon a neurofibrillar net surrounding the lens itself, fibrils also spreading throughout the cytoplasm (Fig. 1B). The cells rest upon the basement membrane and extend about half-way up between the neighbouring epidermal cells.[263] The cells surrounding the photoreceptors are slightly parted, a pinhole of light being permitted to fall upon the cell, so that light is accepted from one direction only. The sensitive areas are not evenly distributed over the worm's body

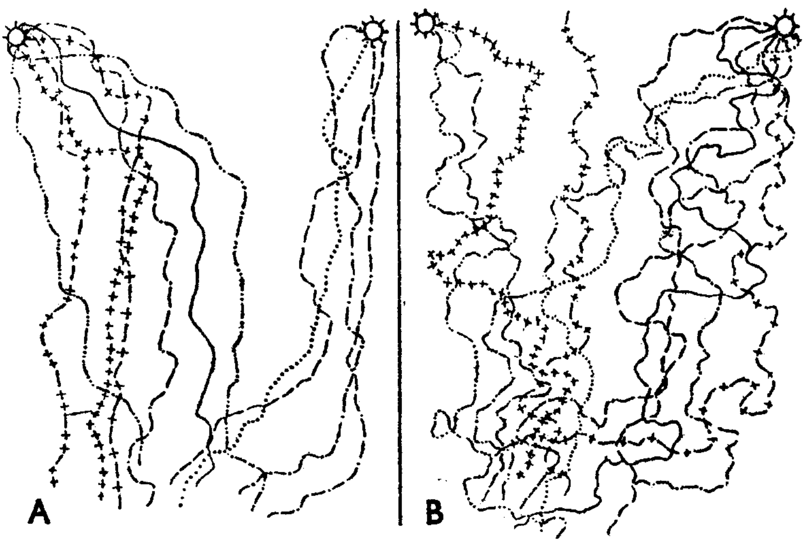


FIG. 2. Tracks of caterpillars of *Lymantria dispar* reacting to two candles, A, normal animals, B, blinded animals. (Lammert[326]).

for there is greater sensitivity at the head end, greatest on the prostomium and declining along the body for a few segments and then increasing in sensitivity to the tail. The dorsal region of any segment is more sensitive than the ventral.[262] Such isolated scattered sensitive cells are common among invertebrates where they are probably the cause of the generalized dermal light sense found in some insects. The cave beetle, *Anophthalmus*, though eyeless as its name implies, will still react to the light of a candle.[354] The caterpillars of various *Colias* species which are coloured to match their surroundings always arrange themselves so that light falls on them from a particular angle. The perception of the direction of the incident light seems to be a property of their body surface, for lacquering their eyes does not affect the reaction. Indeed the caterpillars of a number of moths and butterflies can still orientate to lights with their ocelli covered (Fig. 2).[319] Cockroaches (*Blattella*[211] and *Periplaneta*[62]) though blinded by painting over their eyes will still choose a dark place rather than a light one.

These unicellular eyes are euthoscopic in function as are many of the simpler multicellular eyes. The plan of these simple eyes is a vesicle lined with light-sensitive cells from which nerves lead to the nervous system. Such vesicles occur among the coelenterates, on the margins of the bells of jellyfishes, for example, among annelid and other worms, usually at their anterior ends, among echinoderms, like those at the tips of the arms of starfishes, among molluscs, particularly the gastropods, and finally on the larvae and adults of various insects.

Sometimes the pit is open to the exterior, though its cavity may be full of secretion, as in the eye of *Haliotis*, the ormer. But the pit may also be closed by a transparent or translucent piece of the outer skin which may itself act as a lens, or may enclose a separate lens within the vesicle (Fig. 3A). The eyes of *Helix pomatia*, borne on the ends of the tentacles, contain a spherical lens within a closed vesicle, the inner wall of which is composed of sensitive cells, while the outer wall and the epithelium above are transparent (Fig. 3B).

Where the external layers overlying the eye are thickened and transparent, forming a lens, as they are in an insect's ocellus (Fig. 5B), there is clearly little possibility of any accommodation device for altering the focus. But where the lens is separate and enclosed, muscles attached to it directly or indirectly may be able to alter the properties of the optical system. Ciliary muscles sling the lens in position in the eye of *Sepia officinalis* (Fig. 4B). Their contraction moves the lens towards the retina, while contraction of the muscles of the ocular bulb squeezes the lens forward. Thus the eye can act eidoscopically, a clear image being produced on the retina. The process is indirect in the polychaete, *Alciopa* (Fig. 4A). Lens movement is brought about by the contraction of a fluid-filled ampulla which forces liquid into the optic vesicle, pushing the lens forward. Alteration in the shape of the lens can be produced by the muscles of the corneal bulge which contract upon the body of the lens.

Such vesicular eyes, whether open or closed, are usually backed by a pigment layer permitting light to fall upon the retina from one direction only. The amount of light may be further reduced by a pupillary device, like the stripes threading the surface surrounding the lens of *Alciopa*. In general the retinae have nerves leaving from the outside of the cup, but in the eyes of *Pecten*, the scallop, they leave the retina cells from within, for the cells point outwards, so that light must pass through the network before stimulating the retinal cells (Fig. 3C). The eyes are arranged around the mantle edge

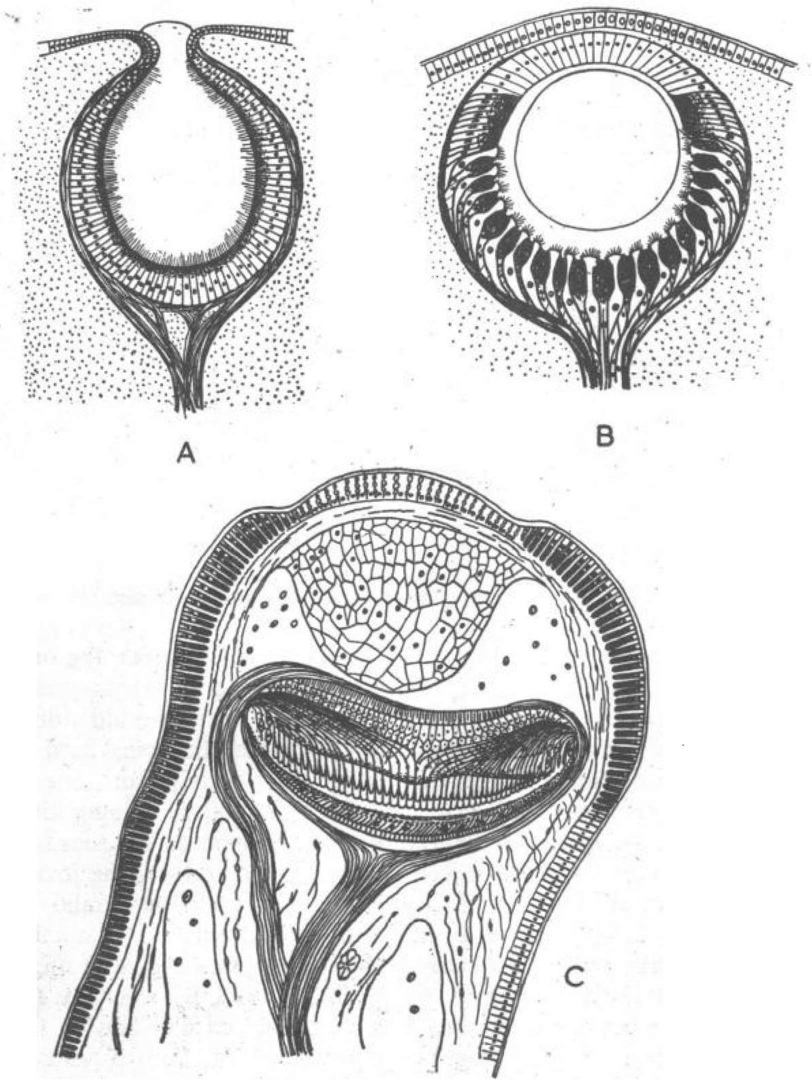
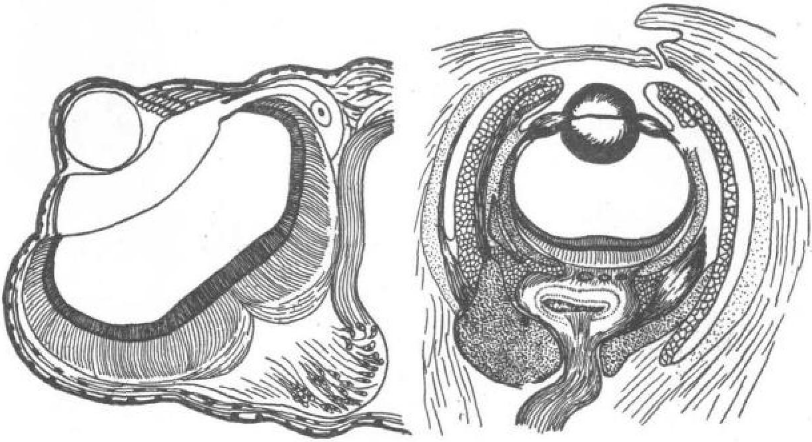


FIG. 3. Sections of the eyes of A, *Haliotis*, B, *Helix pomatia* and C, *Pecten* (from Hesse[263a])

which protrudes from the gaping shells. The retina of planarian worms is also of this type and the orientation of the cell to the light rays determines whether it shall be stimulated or not (see Chapter III).

One of the most efficient and the most widespread pattern of eidoscopic eye is that of the compound eye, found in most arthropods



A B

FIG. 4. Sections of the eyes of A, *Alciopa* and B, *Sepia.*

but particularly among insects. This is composed of units, the ommatidia, each of which is itself a receptor with a fixed focus lens system (Fig. 5A); thus no accommodation is possible within the individual unit. But the eye acts as a whole, all the ommatidia being used in concert. The numbers of these in an eye vary widely from one in the ant, *Ponera punctatissima*, to 10,000–28,000 in dragonflies. Each acts as a receptor for light, any image formed on the sensitive cells not apparently being received as such, but, rather, the image built up from all the units is appreciated. Thus a large number of ommatidia will give rise to an image of finer grain than a smaller number. Ideally for more accurate image perception a greater number of ommatidia are required. A limit is imposed, however, by the optical properties of the system of each individual unit and by the angle between it and the neighbouring ommatidia. Thus a point is reached where closer packing of ommatidia in the same eye, resulting in units of smaller cross-section will lead to a decrease in acuity because of diffraction. In fact examination of a number of eyes of hymenopterous insects has shown that the inter-ommatidial angle is always just below that for the limiting resolving power for the ommatidia in question.[26]

An ommatidium contains a corneal lens (equivalent to the thickening of the epidermis in closed vesicular eyes) with a crystalline cone