CHAPTER VII

THE SYSTEMATIC ANATOMY OF INVERTEBRATE EYES

From the morphological point of view we have seen that the visual organs of Invertebrates show an astonishing range in structure, varying in complexity from the simple eye-spot or the single visual cell to the elaborate organs characteristic of Cephalopods or Insects ; from the functional point of view the variation is equally great, evolving from a primitive and perhaps undifferentiated sentiency which may influence metabolic and motorial reactions, to the capacity to form elaborate images whereby intensity, hue, form and spatial relationships can be differentiated with sufficient exactitude and appreciation to determine behaviour. The curious thing, however, is that in their distribution the eyes of Invertebrates form no series of contiguity and succession. Without obvious phylogenetic sequence, their occurrence seems haphazard ; analogous photoreceptors appear in unrelated species, an elaborate organ in a primitive species [1] or an elementary structure high in the evolutionary scale,[2] and the same animal may be provided with two different mechanisms with different spectral sensitivities subserving different types of behaviour.

A striking example of this is seen in the flat-worm, *Planaria lugubris*, which has both positive and negative photo-reactions (Viaud and Médioni, 1949) ; if this animal is bisected the photo-positive reactions appear in the posterior segment before the nerves regenerate suggesting that these responses are due to dermal sensitivity, while it has been shown that the photo-negative reactions are due to the eyes ; photokinesis is dependent on the skin, positional orientation to light on the eyes. In the earthworm, *Lumbricus terrestris*, on the other hand, the photo-negative reactions in bright light are controlled by the head-ganglion, while the photo-positive reactions in dim light are mediated by the ventral cord ; the two activities are mutually antagonistic but normally the cephalic mechanism is dominant (Prosser, 1934). Again, the possession of both ocelli and compound eyes by many insects, the first sometimes reacting to polarized light and orientative in function, and the second to ordinary light as well and also subserving form vision, is an example of two mechanisms which are supplementary in function and not antagonistic (Wellington, 1953).

We shall now discuss the occurrence of these organs in the invertebrate phyla, referring back to the previous chapter for a description of their minute structure.

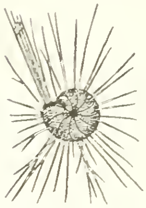
[1] Such as the complex eye of the jelly-fish, *Charybdea* (p. 183).
[2] Such as the simple eyes of Insects (p. 224).

TYPICAL PROTOZOA

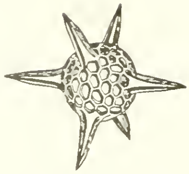
[*Drawn not to scale, but approximately to a standard size.*]

SARCODINA

Amœba



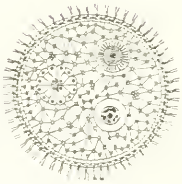
Foraminifer



Radiolarian shell

FLAGELLATA

Euglena

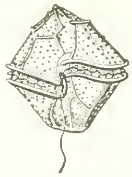


Volvox

Trypanosoma

Trichomonas

Noctiluca
(see Fig. 886)



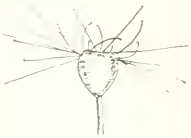
Gonyaulax
(Dinoflagellate)

CILIOPHORA

Paramœcium

Vorticella

Stentor



Suctorian

SPOROZOA

Sporozoite
of
Plasmodium

Protozoa

PROTOZOA are the most primitive and simplest of animals, some of which might with equal justification be considered as plants ; they are essentially single-celled but sometimes form loose colonies by budding or by cell-division, showing some degree of co-ordination but never forming differentiated tissues. Of all animal types they are the most numerous, being found in every continent, on land, in fresh water, in the seas and impartially distributed as parasites within all animals (including some of their own kind), among which not the least frequented is Man ; their skeletons contribute largely to the oozes of the seas and to the composition of the rocks of which the land-masses are made.

Within the phylum four methods of activity are evident—amœboid movement, flagellate and ciliary progression, and encystment with spore-formation, characteristics under which the upwards of 15,000 species may be conveniently grouped into 4 classes (see p. 179).

SARCODINA (or RHIZOPODA), organisms which progress by sending out finger-like pseudopodia into which the protoplasm of the cell pours itself. This class comprises such types as the fresh-water *Amœba*, the parasitic *Entamœba* or the marine Foraminifera with chalky shells and Radiolaria with siliceous shells which after death enter largely into the formation of the oozes of the bed of the ocean.

FLAGELLATA (or MASTIGOPHORA), organisms which swim by the lashing movements of one or a few whip-like flagella. The class comprises such types as the common *Euglena* and colonial forms such as *Volvox* almost universal in fresh-water ponds, the parasitic, disease-producing Trypanosomes and Trichomonads, Dinoflagellates including *Noctiluca* which gives luminescence to the seas,[1] and Cystoflagellates, important constituents of the plankton of lakes and the oceans.

CILIOPHORA, organisms which progress by the coordinated movements of many hair-like cilia. The class comprises the Ciliates (such common types as the slipper-shaped *Paramœcium*, the bell-shaped *Vorticella* or the trumpet-shaped *Stentor*) and the Suctorians which lose their cilia in adult life and in their place develop tentacles used as suckers by which they capture and suck out the bodies of their protozoan prey.

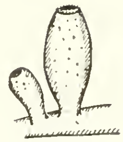
SPOROZOA, encysted organisms without a locomotive mechanism ; they are parasitic on almost every species of animal and are spore-forming in habit (Coccidia, Hæmosporidia, *Plasmodium*, etc.).

In view of the fact that the response to light in these primitive forms is motorial, it is not surprising that receptors are not found in the passive parasitic Sporozoa ; in the first three classes responses to light are found among the freely-swimming active types, but as would be expected in unicellular organisms, the receptor mechanisms are of the most primitive nature. In the Sarcodina (*Amœba*) and some Ciliates

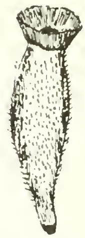
[1] p. 738.

(*Paramœcium*) sensitivity to light is diffuse ; in other Ciliates (*Stentor*) it is localized to a part of the organism but without apparent specific mechanism ; but even at this primitive unicellular stage an obvious localization of function may be attained by the development of an EYE-SPOT and the efficiency of the organelle increased, particularly in the acquirement of a crude directional appreciation, by the provision of pigment (as in *Euglena*) [1] or even of a primitive refractile mechanism (as in some Dinoflagellates).[2]

Parazoa



Leucosolenia



Sycon

The SPONGES (PORIFERA), sessile marine animals which form living thickets in the sea, represent a cul-de-sac in evolution between Protozoa and Metazoa dating back almost to the beginning of geological records. They are the simplest multicellular animals and show the beginnings of the development of a "body" composed of tissues ; but although there is cellular differentiation there is little cellular co-ordination. Being vegetative and sedentary in habit they have no need of sense-organs as they lie moored to rocks or sea-weed. They possess no nerve cells but the body cells retain properties of an irritability of a low level ; and in the active larval forms of certain types (the simple sponge, *Leucosolenia*) apolar light-sensitive cells of the most elementary type have been described (Minchin, 1896).

Invertebrate Metazoa

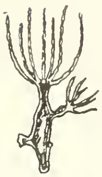
In Metazoa—which includes all animal species apart from the Protozoa and Parazoa—the development of specialized cells and their eventual co-ordination into distinct organs allow the evolution of specific sensory activities as the term is generally understood. These we shall now study, but it must be remembered that the Invertebrates (or Non-chordates) do not form a homogeneous sub-kingdom but rather represent an assemblage of unrelated groups of animals which have little in common except the negative attribute of not being provided with a dorsal nerve-cord with its supporting axis or with gill-slits. From our restricted point of view there is the dramatic difference that (with few exceptions) the eye when present is developed from the skin, while in Vertebrates it originates as an outgrowth of the brain.

CŒLENTERATA

CŒLENTERATES are simply formed animals with a body-cavity (cœlom) and digestive cavity (enteron) combined so that the body is formed as a sac with an opening at one end only. They show the beginnings of separate organs with a consequent division of labour, and among them

[1] p. 126. [2] p. 126.

visual structures of some complexity first make their appearance. The phylum may be divided into two sub-phyla—the CNIDARIA, provided with numerous stinging cells (κνίδη, a nettle), and ACNIDARIA, wherein these are replaced by adhesive cells. The first-sub-phylum is divided into 3 classes :



Hydra

HYDROZOA, comprising solitary polyps such as the fresh-water *Hydra*, the marine Hydroids, branching colonial polyps of vegetative appearance liberating freely-swimming Hydromedusæ (*Obelia*, *Sarsia*, etc.) and some pelagic colonial forms.

SCYPHOZOA (" cup animals "), marine jellyfish, free-swimming medusæ, typically umbrella-shaped with the important organs situated on the margin or under-surface.

ANTHOZOA (" flower animals "), sessile marine polyps with no medusa-forms, such as sea-anemones, sea-fans, sea-pens and corals.

Obelia medusoid

ACNIDARIA, comprising the Ctenophora (comb-jellies or sea-gooseberries), delicate freely-swimming globular organisms, pelagic in habit, gelatinous and transparent, beautifully iridescent in the sunlight and often luminescent in the dark,[1] provided with comb-like rows of cilia.

Obelia polyp

The degree of elaboration of the visual receptors varies with the motility of the organism, and many Cœlenterates are sessile, plant-like zoophytes ; eyes are therefore confined to the mobile medusæ and these are of a very primitive nature,[2] while the sessile polyps of this phylum (hydroid forms and all Anthozoa) have no sense organs or, at most, contact photoreceptors of the most elementary type.[3]

The Ctenophora are provided with a sense organ at the upper pole of the organism consisting of a mass of limestone particles supported on cilia associated with sensory cells communicating by nerve fibrils with the swimming-combs; this is considered to act as a statocyst or balancing device and visual organs are absent.

Sea-anemone

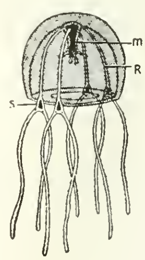
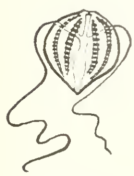


FIG. 162.— THE MEDUSOID FORM OF *BOUGAINVILLEA* (*MARGELIS*). M, manubrium; R, radial canal ; S, sense organ (after Allman).

Among the Hydrozoa, some fresh-water forms are sensitive to light but possess no detectable visual organs ; a hydra, for example, will migrate towards the lighted side of its container where, incidentally, there are usually more food-organisms. In some freely-swimming Hydromedusæ, however, externally visible light-sensitive organs provided with sensory cells and pigment and sometimes a refringent apparatus may be found in the tentacular bulbs at the bases of the tentacles (Fig. 162) ; these take the form of



Comb jelly (see Figs. 887–8)

. 739.
r detailed information, see O. and R. Hertwig (1877), Schewiakoff (1889), Berg 898), Linko (1900), v. Uexküll (1909), Lehmann (1923).
16.

a primitive flat eye, as in *Turris* or *Lizzia* (Fig. 96), or are invaginated as an elementary cupulate eye, as in *Sarsia* (O. and R. Hertwig, 1878 ; Jourdan, 1889). These organisms are light-sensitive and extirpation of the tentacular bulbs with the ocelli completely abolishes the response to light.

Among the jellyfish (Scyphozoa) more elaborate organs are seen. In the common jellyfish, *Aurelia aurita*, which is found in great shoals around the British coast, eight sense-organs (TENTACULOCYSTS) arise as modifications of tentacles ; each, lying in the protection of a marginal

FIGS. 163 AND 164.—THE COMMON JELLYFISH, *AURELIA AURITA*.

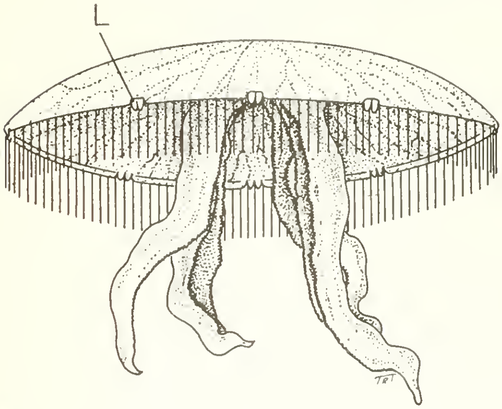


FIG. 163.—Side view of the jellyfish, showing the numerous marginal tentacles hanging from the border of the convex umbrella, and the dependent oral arms. The margin of the umbrella is broken by 8 notches, the marginal lappets (L).

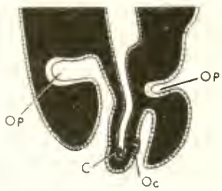


FIG. 164.—A marginal notch, showing a tentaculocyst comprised of two olfactory pits, OP, a calcareous concretion, C, and an ocellus, OC (modified from Lankester).

niche, has three types of sensory cells—red or black pigmented cells responding to light, "olfactory" cells with a chemical appreciation, and club-like cells containing calcareous concretions with a balancing function (Figs. 163–4).

Exceptionally, as in the Cubomedusan, *Charybdea*, a large ocellus has been reported with a cellular lens, a vitreous structure and a complex retina—an organ structurally capable of some degree of visual imagery (Fig. 102) (Schewiakoff, 1889 ; Berger, 1898). The biological value of this elaboration in a brainless organism is somewhat speculative.

ECHINODERMATA

Among ECHINODERMS ("spiny skinned"), a phylum characterized by its radial symmetry, visual organs are rudimentary. This would

Starfish

Brittle-star

be anticipated from the absence of centralization in the nervous system, associated presumably with the absence of a head region, and from the characteristically sluggish and sedentary habits of its members. The phylum is divided into 5 extant classes :

ASTEROIDEA, or starfishes, motile but sluggish organisms.

OPHIUROIDEA or brittle-stars, resembling starfishes but with the arms sharply marked off from the central disc.

ECHINOIDEA or sea-urchins, living off rocky coasts, with a round pin-cushion-like body covered with plates and provided with long sharp spines.

HOLOTHUROIDEA or sea-cucumbers, worm-like creatures with calcareous plates, occurring in most seas.

CRINOIDEA, sea-lilies or feather-stars, stalked forms anchored on rocks or

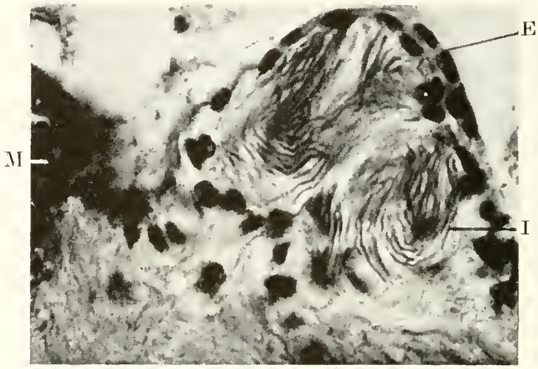
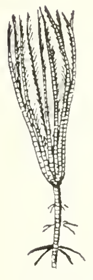


FIG. 165.—THE IRIDOPHORES IN THE SEA-URCHIN, *DIADEMA ANTILLARUM*.

Section through a cluster of iridophores, I ; E, epidermal layer ; M, melanophores, underneath which lies the superficial nerve layer (fixed Bouin ; stained Masson's argentaffine reaction ; counter-stained Mallory's triple stain. (Approx. × 500) (N. Millott).

in mud usually at great depths, with appendages (cirri) and branching arms growing from a central cup ; feather-stars become free-swimming in adult life.



Sea-lily

In most Echinoderms the skin is diffusely sensitive to light, particularly in sea-cucumbers (Crozier, 1914–15) ; in brittle-stars and feather-stars there are no special sense organs ; in sea-cucumbers sense organs are represented by statocysts sometimes present at the bases of the tentacles, and tactile processes sometimes present on the dorsal surface of some of the creeping forms ; " eyes " are present only in starfishes.

Free-swimming feather-star

The diffuse dermatoptic sense shows interesting variations. Thus in some starfishes the body-surface is said to be sensitive to changes in intensity, the podia and skin gills to steady light ; in some sea-cucumbers (*Synapta*) the whole surface is sensitive to both, while in others (*Holothuria surinamensis*) the rim of the cloaca is particularly sensitive, the posterior end and tentacles less so and the podia least. In the sea-urchin, *Paracentrotus lividus*, the apical poles are

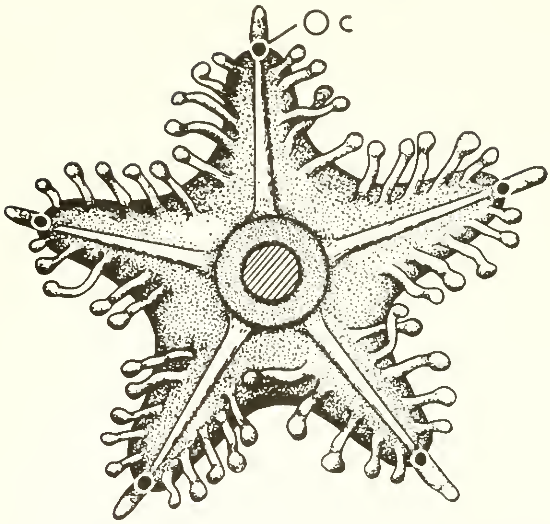
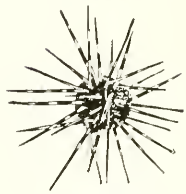


FIG. 166.—DIAGRAM OF A VERY YOUNG ASTEROID

At the base of the 5 terminal tentacles is an optic cushion with a bright red ocellus, Oc, connected by an epidermal radial nerve which runs to the central nerve pentagon surrounding the mouth (after Lang). Compare Plate I.

Sea-cucumber, *Holothuria*



The sea-urchin, *Diadema*

said to show the most rapid reactions (Scheer, 1956). In the Echinoid, *Diadema*, the distribution of sensitivity corresponds to the distribution of the nerve elements and it may be that these are directly stimulated by light as we have seen to occur in the apolar light-sensitive cells of worms (Millott, 1954). On the other hand, photosensitive pigments may be present in minute quantities, but there is yet no evidence as to their nature.

Many SEA-URCHINS have the same primitive sensitivity associated particularly with their pigmented spicules which move on the stimulus of light (v. Uexküll, 1900), and in some types characteristic iridescent bodies associated with melanin pigment lie near the spines (*Diadema antillarum*) (P. and F. Sarasin, 1887 ; Dahlgren, 1916 ; Millott, 1950–54). These represent clusters of regularly arranged plates resembling iridophores [1] in their arrangement, which presumably act by reflecting the light onto the sensitive spines (Millott, 1953) (Fig. 165). It is of historical interest that the Sarasins (1887), in a much quoted paper, described similar structures in *Diadema setosum*, an allied species inhabiting the Indian Ocean, as being "eyes" composed of several hundred polygonal corneal facets, a vitreous-like jelly and a "retina", but without nerve fibres.

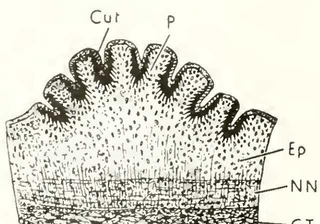


FIG. 167.—The optic cushion of the Asteroid

Cut, cuticle ; CT, connective tissue ; Ep, epithelium ; NN, nerve-net ; P, pigment cells.

In STARFISHES (Asteroids such as the common five-rayed *Asterias*), although the skin is often diffusely light-sensitive, on the tip of each of the five arms a visual

[1] Compare iridocytes, p. 89.

organ is formed as a modified tube-foot lying on a slight elevation (the " optic cushion ") on the dorsal surface of the terminal ossicle (Fig. 166). The organ is bright red due to the presence of β-carotene and esterified astaxanthin and consists of an aggregation of several cupulate ocelli of the simplest type covered by cuticle and lined by sensory and pigmented cells (Plate I ; Fig. 167) (Pfeffer, 1901) ; a central lenticular body may serve to concentrate light upon the receptive elements (van Weel, 1935 ; Smith, 1937). The optical function of this organ in *Asterias* has been convincingly demonstrated by Hartline and his co-workers (1952) who recorded the electric impulses following stimulation by light. The terminal tube-foot appears to be olfactory in function.

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WORMS

The large group of " WORMS " shows a variety of visual organs as pleomorphic as the multitude of forms which constitute this loose grouping of animals, showing every variation from a unicellular eye to a relatively complex organ. In some cases the surface of the whole body seems to be sensitive to light and it has not been possible to identify specific sensory cells ; in most cases, however, specialized sensory structures occur, for the elucidation of which we are largely indebted to the classical work of Richard Hesse (1899–1908). Their presence, their number, and the degree of their differentiation vary with the animal's mode of life. This is the lowest group in the animal kingdom to show bilateral symmetry and the sense organs share in this general scheme of distribution ; moreover, these organs are usually concentrated towards the head-end of the animal where they are of greatest biological value.

PLATE I

The Light-sensitive Apparatus of the Starfish

Fig. 1.—*Marthasterias glacialis*, showing the position of the eye-spot, *e.s.*, one of which is present at the tip of each of the five arms.

Fig. 2.—The excised eye-spot (optic cushion) showing the optic cups, *o.c.* They have a striking red colour due to *B*-carotene and esterified astaxanthin; it is to be noted that some of the colour of the body-wall, which is also light-sensitive, is due to the same pigments (N. Millott, *Endeavour*, 1957).

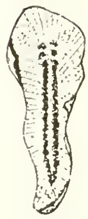
[*To face p.* 186.

These photoreceptors are of the most varied types and many species possess eyes of more than one variety. The neuro-sensory cells may be either apolar in type provided with an internal optic organelle, or bipolar, provided with a ciliated or striated border [1]; they may occur as single cells or in groups forming an eye of either the subepithelial or epithelial variety, in which case it may show a flat, cupulate or vesicular arrangement. Pigment is a constant association, situated within the sensory cells or in special supporting cells. If a refractive medium is present it may be formed either from the retinal or the epidermal cells, while light-refracting structures are usually cuticular in origin. As a general rule their function can only be the primitive ability to detect light, but the visual organs of some types, such as some polychæte worms, are structurally capable of some degree of localization and resolution (a *directional eye*) and perhaps even of visual imagery.

UNSEGMENTED WORMS

The unsegmented worms may be divided into three phyla—flat-worms, ribbon-worms, and thread-worms.

1. PLATYHELMINTHES or FLAT-WORMS constitute a group of very simply organized creatures the members of which show the progressive degeneration associated with parasitism. It is divided into 3 main classes :



Polyclad, *Leptoplana*

(*a*) TURBELLARIANS, freely-swimming leaf-shaped aquatic creatures of carnivorous habit, frequenting brackish or salt water or moist places on land ; the name is derived from the turbulence caused in the water by the beating of their cilia when they swim. They are classified according to the arrangement of the gut the minute marine Acœla (without intestine), the small salt and fresh-water Rhabdocœla (rod-shaped intestine), the (mainly) marine Allœocœla (irregular intestine), the small, flat, elongated Tricladida (3-branched intestine) found in fresh or salt water or on land (including the Planaria), and the large, leaf-like, marine Polycladida (many-branched intestine).

(*b*) TREMATODES or FLUKES, leaf-like parasites, external or internal, found on or in all types of Vertebrates, clinging to their hosts with suckers. Examples are the liver-fluke, *Fasciola hepatica*, which infests the livers of sheep and cattle, or the *Schistosoma hæmatobia* which causes bilharziasis.

Schistosoma

(*c*) CESTODES or TAPE-WORMS, endoparasites, frequenting the alimentary canal of Vertebrates, including domestic animals and man, such as *Tœnia echinococcus*, or *T. solium*.

2. NEMERTINES or RIBBON-WORMS, ribbon- or thread-like in shape, often vividly multi-coloured, varying in size from under an inch to enormous lengths (25 metres in *Lineus*) and provided with cilia and a remarkable retractile proboscis forming a tactile organ used to capture prey. Most are marine in habitat, creeping in the mud and under stones ; a few are found in fresh-water (*Prostoma*); some are terrestrial (*Geonemertes*) ; and a few live commensally with bivalves or ascidians.

Tœnia echinococcus

3. NEMATODES, ROUND- or THREAD-WORMS, cylindrical in shape and often minute, which teem in the soil or in water and are often endoparasitic in plants and animals (*Ascaris, Trichinella, Ankylostoma, Filaria*, etc.) ; but free-living forms occur at any rate in part of the life-cycle.

[1] p. 127.

The PLATYHELMINTHES have sense organs only of the most rudimentary type—if any. The freely-living TURBELLARIANS (Planarians, etc.) are the most adequately equipped with eyes (Figs. 168 to 170). These may be merely two or four in number, in which case they lie on the dorsal aspect of the head-end associated with the tentacles near the cerebral ganglion, as in the fresh-water Rhabdocœla ; but others such as the marine Polycladida may possess several hundred. A common arrangement, well seen in the Tricladida, is that these multiple ocelli are distributed around the circumference of the body concentrated particularly at the anterior margin (Figs. 168 and 170) (Busch, 1851 ; Hyman, 1938–51). The eyes are always very elemen-

FIGS. 168 TO 170.—THE EYES OF TURBELLARIAN WORMS.

FIG. 168.—A land planarian, *Geoplana mexicana*.

There is a row of eyes along the entire margin of the animal (after Hyman).

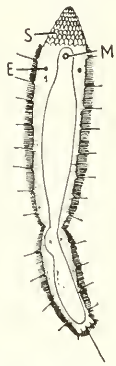


FIG. 169.—The eyes of the pelagic Rhabdocœle, *Alaurina prolifera*.

S, papillated snout ; M, mouth ; E, paired eye (after Busch).

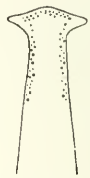


FIG. 170.—The eyes of the fresh-water planarian, *Polycelis coronata*. They are concentrated at the head-end (after Hyman).

tary, and lacking a dioptric apparatus are capable only of light perception although a directional appreciation may be evident (Taliaferro, 1920). The number of visual cells is said to vary between 1 and 200 (Hesse, 1896 ; Schmidt, 1902). Occasionally, as in *Dendrocœlum*, they are of the flat epithelial type (Fig. 95). Usually they are of the subepithelial type, appearing as minute pigmented spots about 0·1 mm. in diameter and consisting of a pigmented goblet enclosing the sensory cells (Figs. 91 and 92). In these the sensory cells are of the bipolar type with a striated margin facing away from the direction of light to form an inverted retina. When the eyes are near the cerebral ganglion the sensory fibres enter the latter directly ; otherwise they enter the peripheral nerve-net.

Dendrocœlum

In some Rhabdocœla (*Stenostonum*) curious hemispherical bodies consisting of refringent granules lying underneath a bowl-shaped mass have been credited with a photosensitive function ; there is no good evidence, however, for this assumption.

Eyes are lacking in the cave-dwelling planarians (Kenkiidæ) and in endoparasitic Rhabdocœla.[1]

Fasciola hepatica

TREMATODES may possess simple ocelli in the larval stage (as in the liver-fluke, *Fasciola hepatica*), but the adults, leading an essentially parasitic existence, rarely possess sense organs. If they are present they are of the simplest type, usually consisting of a single cell with a striated border invested by a cup of pigment (Hesse, 1897 ; André, 1910 ; Faust, 1918) ; a typical example is seen in the unicellular eye

FIGS. 171 AND 172.—THE EYES OF NEMERTINE WORMS.

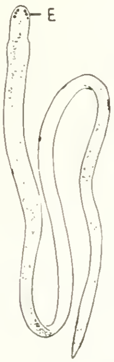


FIG. 171.—*Lineus ruber*. E, eyes (after Hyman).

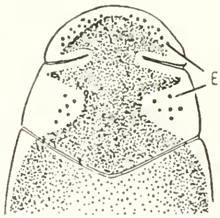


FIG. 172.—The head of *Amphiporus angulatus*. E, eyes (after Hyman).

of *Tristomum papillosum*, a marine Trematode parasitic on fishes (Fig. 87).

CESTODES, in keeping with their endoparasitic life, are without sense organs.[2]

Among the NEMERTINES, most of which are freely-living and marine in habitat, rudimentary eyes of the same subepithelial type as occur in flat-worms are general and occasionally are very numerous (Figs. 171–72). They are always limited to the anterior end of the animal. Some species possess two eyes, others four or six on the prostomium ; others up to 250 eyes (*Amphiporus*) arranged in clusters or rows, while the number may vary in different individuals of the same species. The eyes are nearly always subepithelial in type consisting of bipolar cells terminating in a brush border enclosed within a pigment cup of epithelium (Hilton, 1921) (Fig. 93). The eyes of the terrestrial genus,

Amphiporus

[1] pp. 724, 733.   [2] p. 734.

Geonemertes, differ from the usual type. In these the pigmented epithelium forms a complete circle within which is a mass of refractile material ; the nuclei of the sensory cells are arranged outside the circle of pigment and their distal terminations pass through it into the central refractile mass (Schröder, 1918).

Nematode, *Ascaris*

In the NEMATODES, the majority of which are endoparasitic, sense organs are limited to papillæ on the lips ; in the free-living sexual state, however, rudimentary eyes may exist, consisting of a lens-like cuticular body resting on a cup of pigmented cells (Steiner, 1916 ; Hilton, 1921 ; Schulz, 1931).

SEGMENTED WORMS (ANNELIDS)

The segmented worms exhibit much diversity in habit and structure but their essential characteristics are segmentation of the body with paired appendages on each segment and a closed vascular system. Annelids are found both in marine and fresh water and on land, and in the entire phylum more than 6,500 species are known. These are divided into 4 classes, the first two of which are provided with chitinous bristles or setæ for locomotion.

Arenicola

1. OLIGOCHÆTES (with few setæ), hermaphroditic creatures, essentially terrestrial in habit, typified in the common earthworm, *Lumbricus terrestris*, or the tiny aquatic mud-worms living in brooks or between tide-marks.

2. POLYCHÆTES (with many setæ), essentially marine in habit ; in them the sexes are separate. Two types exist, distinguished by their habits. The more active forms (ERRANTIA) are typified in the common lob-worm, *Arenicola marina*, found burrowing in sandy beaches, or the freely-swimming types, such as the rag-worm, *Nereis*. The sedentary forms (SEDENTARIA) are tubicolous in habit leading a sluggish life within tubes, limy, sandy or gelatinous ; as an adaptive characteristic the tentacles, gills and sensory organs are aggregated in the anterior part of the worm which protrudes from the tube.

3. ARCHIANNELIDS comprise a small and anomalous class of simple marine worms with juvenile characteristics and without setæ, freely swimming or burrowing in sand and gravel.

4. HIRUDINES OR LEECHES form a highly specialized and much modified class, most of which live in fresh water in ponds or sluggish streams although a few are marine and others (the wiry land-leeches of the Far Eastern jungles, *Hæmadipsa*) are terrestrial, living in moist places. In habit they are greedily suctorial, sucking the blood of fishes, amphibians or other victims.

Hæmadipsa

Eyes are usually lacking in the OLIGOCHÆTES ; of those possessing visual organs, the most typical example is the earthworm, *Lumbricus terrestris*. Its unicellular light-sensitive organs distributed in the epithelium and aggregated around subepithelial nerves have already been fully described [1] (Figs. 86, 88). These visual elements are situated where they are of the greatest biological value, being concentrated at the two extremities, particularly the anterior.

Lumbricus

[1] p. 131.

Thus W. N. Hess (1925) found that in the prostomium there were some 440 light-sensitive cells in the epidermis and 700 situated in nearby nerve enlargements, while in subsequent segments they were much fewer. Their relative numbers in corresponding small areas ($200 \times 300\mu$) on the dorsal surface of the animal are as follows—in the prostomium, 18 ; 1st segment, 10 ; 2nd segment, 5 ; 3rd segment, 3 ; 40th segment, 0 ; antepenultimate segment, 1 ; penultimate segment, 1 ; last segment, 4. The segmental photic sensitivity varies directly with the number of receptors, and the distribution of light-sensitive elements conforms with the habits of the earthworm.[1]

Among POLYCHÆTE WORMS, the burrowing lob-worm, *Arenicola marina*, is not provided with visual organs although the prostomial

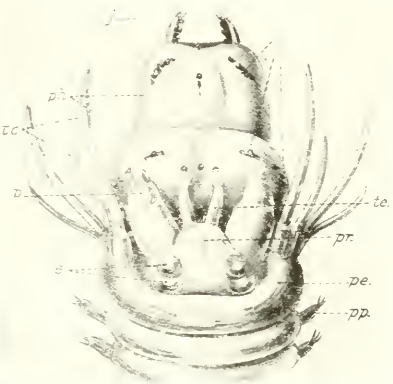
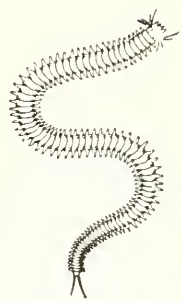


FIG. 173.—THE HEAD OF *NEREIS*, SHOWING THE FOUR EYES.

e, eyes ; *j*, jaw ; *p*, palp ; *pe*, peristomium (first two segments fused) ; *ph*, pharynx ; *pp*, first ordinary parapodium ; *pr*, prostomium ; *t*, accessory teeth ; *tc*, tentacular cirri ; *te*, tentacle. (From Borradaile's *Manual of Elementary Zoology* ; Oxford University Press.)

lobes are diffusely sensory. In contrast with the burrowing type, however, the freely-swimming marine polychætes show a much richer development (Fig. 173). Of these, *Nereis* is a typical example. This worm has four prominent eyes situated on the prostomium, each of the cupulate type with a cuticle externally and a retina internally formed of well-developed sensory cells with rod-like receptor endings (Fig. 101). Other forms, such as *Polyophthalmus*, have in addition to the prostomial eyes similar pairs of subepithelial organs in many segments of the body ; such eyes[2] are formed sometimes on each segment (*Myxicola æsthetica* ; *Eunice*), and occasionally on the anal segment (*Fabricia*).



Nereis

A much more complex type of eye of the vesicular type is found

[1] p. 572.

[2] These organs, usually considered to be " eyes " are said by some to be light-producing (p. 736) (Benham, 1896).

in certain pelagic polychætes such as *Alciopa* and *Eupolyodontes*, the intimate structure of which has already been described.[1] These worms have two eyes, sometimes facing forwards (*Eupolyodontes*), sometimes diverging widely (*Alciopa*) (Fig. 174). Each organ is provided with an elaborate retina, a lens, an accommodative mechanism and extra-ocular muscles suggesting the potentiality for binocular vision, an equipment which seems capable of considerable visual powers approximating those of the Cephalopods.[2] Little, however, is known of the habits of these worms.

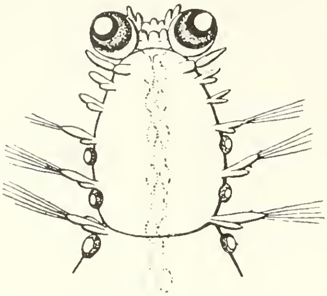
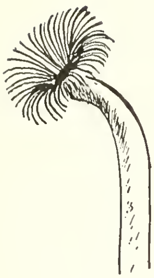


Fig. 174.—The Anterior End of the Polychæte Worm, *Alciopa*.

Showing the two large eyes (after Greeff).

In the sedentary tubicolous polychætes (*Potamilla*, *Branchiomma*, *Dasychone*, etc.) the ocelli are frequently grouped in masses on the branchial filaments to form a composite simple eye of great complexity (Brunotte, 1888 ; Andrews, 1891 ; Hesse, 1896) (Figs. 175 and 176) ; *Vermilia infundibulum* has at least 220 ocelli on the external aspect of each branchium, a total of some 11,000 eyes (Parker and Haswell, 1940). These creatures live within their tubes from out of which extend the branchial plumes bearing the filaments on each of which there is one or more such eyes (Figs. 128, 129). The curious thing, however, is that in



Branchiomma

Figs. 175 and 176.—The Complex Eyes of Tubicolous Polychætes.

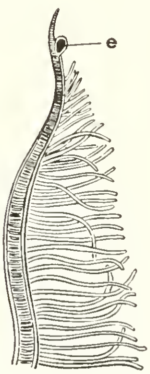


Fig. 175.

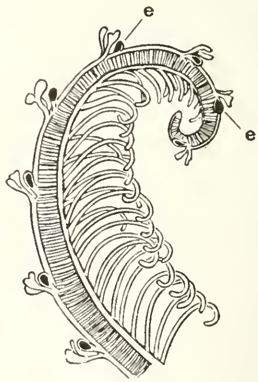


Fig. 176.

The secondary filaments are seen issuing horizontally from the central axis of the branchial filament. Fig. 175, *Branchiomma*, showing the single complex eye, *e*, near the termination of the central axis. Fig. 176, *Dasychone*, showing the row of complex eyes (2 of which are marked *e*) running up and down the central axis (after Benham, *Camb. Nat. Hist.*).

[1] p. 143. [2] Fig. 112.

Branchiomma, at any rate, these structures do not seem to be essential for the most characteristic responses of the worm to changes in the intensity of light (Millott, 1957) ; the position is therefore somewhat anomalous.

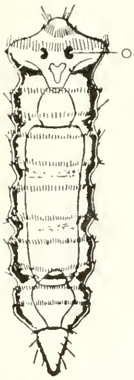
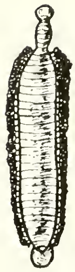


Fig. 177.—The rchiannelid, *Dinophilus*.

Showing the paired ocelli, Oc (after Sheldon-Harmer).

In the simple marine archiannelids, eyes of a similar type are found. In *Dinophilus*, for example, a minute worm found among algæ, two kidney-shaped pigmented eyes are found on the prostomium (Hilton, 1924) (Fig. 177).



Branchellion

Hirudo

leeches (hirudinea) may be provided with visual organs of a simple type varying in number from 2 to 10 (Hesse, 1897 ; Herter, 1932) ; they are incapable of optical imagery although highly light-sensitive, but in some species may be absent. They are found near the anterior extremity of the body and vary considerably in their morphology, but the visual cells are always of the spherical apolar type with a central optic organelle (Figs. 178–9).

In *Branchellion* these organs are unicellular; in *Piscicola* they consist of 12 cells arranged in a row surrounded by pigment. In *Hæmopis* both unicellular and multicellular ocelli are found (Fig. 179). In the common medicinal leech, *Hirudo medicinalis*, there are segmental papillæ with a sensory function on the middle ring of each of the 26 segments. Although all the sense organs are serially homologous the pairs on the dorsal surface of the first five segments are purely visual, constituting ten "eyes" (Fig. 90), provided with a rich nerve supply to the cerebral ganglia. At the other extremity the

Figs. 178 and 179.—The Eyes of Leeches.

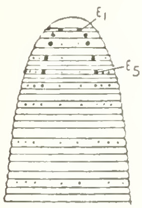


Fig. 178.—The head end of the medicinal leech, *Hirudo medicinalis*.

The dorsal aspect. The body is divided into segments, each of which contains 5 rings (annulæ). In the middle ring of each segment the segmental papillæ have a sensory function. The first 7 (and the last 3) segments have less than the normal number of rings, and the first 5 show two paired eyes as larger black spots, E_1 to E_5, serially homologous with the sensory papillæ (see Figs. 89–90) (after Parker and Haswell).

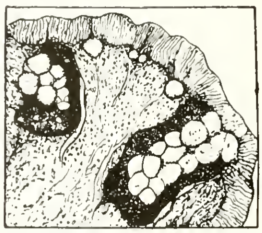


Fig. 179.—Solitary and aggregated eyes of the horse-leech, *Hæmopis sanguisuga* (after Kappers).

organs are probably purely tactile, and between these two regions the sense organs are compound since they contain both visual and tactile cells (Fig. 89).[1]

Subsidiary Invertebrate Phyla

For convenience, four small and subsidiary phyla of the Invertebrates are most usefully considered here.

Chætognath, *Sagitta*

CHÆTOGNATHA ("bristle-jawed") or ARROW-WORMS, delicate, translucent torpedo-shaped creatures comprising some 30 species which swim in incredible numbers in great shoals among the plankton of all seas, have well-developed eyes. *Spadella*, for example, or *Sagitta*, has two composite simple eyes at the anterior extremity of its body, formed by the union of 5 ocelli, the structure of which has already been described (Fig. 132) ; although presumably tripartite, the nerve fibre from each eye is gathered into a single optic nerve trunk.

FIGS. 180 AND 181.—THE EYES OF ROTIFERA.

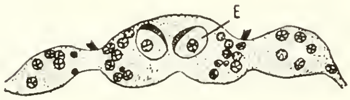


FIG. 180.—The cerebral eye.

Section through the cerebral ganglion of *Synchæta*, showing two cerebral eyes, E (after Peters).

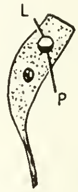
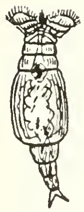


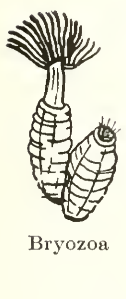
FIG. 181.—The frontal eye.

The eye of *Rhinoglena* with pigment spot, P, and refractile lens, L (after Stossberg).



Rotifer

ROTIFERA ("wheel-bearers"), the beautiful minute wheel-animalcules, sometimes of fantastic shape, which swim so abundantly with the aid of a crown of cilia like revolving wheels in fresh water, damp moss or the sea all the world over, are usually highly light-sensitive. There is a generalized dermatoptic sense which evokes a positive phototaxis, but exact orientation is determined by the eyes and varies with their morphological development (Viaud, 1938–43). Frequently there is a single or paired CEREBRAL EYE embedded in the dorsal nerve ganglion (*Synchæta*) (Fig. 180). In other species, sometimes in addition to the cerebral eyes, there is one or two frontal or lateral eyes (Fig. 181). The cerebral eye consists of a single cell resembling a brain cell ; the lateral or frontal eyes are epidermal cells inside which is a lens-like body associated with a mass of red pigment (Peters, 1931 ; Stossberg, 1932). *Branchionus*, one of the commonest members of this class which inhabits ponds and ditches in abundance, has a simple unpaired eye surrounded by red pigment and associated with tufts of sensory hairs, situated where the cerebral ganglion comes into contact with the body-wall just behind the wheel of cilia at the anterior end of the animal.



Bryozoa

POLYZOA (BRYOZOA), very ancient plant-like organisms which include fresh-water and marine forms (sea-mats, etc.) are sessile colonial corallines or "moss animals" which grow in tufts on the shores or in pools all over the world encrust-

[1] p. 133.

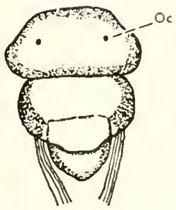
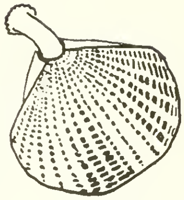


FIG. 182.—THE OCELLI (Oc) OF THE LARVA OF THE BRACHIOPOD, *CISTELLA* (after Gladstone).

ing seaweed, rocks and piles with a lace-like coating, and multiply by budding. Some 1,800 species have been described. The larvæ of some species during their short freely-swimming life before they settle on the rocks or mud, are sometimes provided with rudimentary eyes. Thus the larvæ of *Bugula turrila* which have 4 or 5 slender flagellæ, have 4 brilliantly red spherical eye-spots, 2 close to the pyriform organ and 2 larger eye-spots located in the opposite hemisphere. The larva of the American *Bugula flabellata* has no light-sensitive organs, but the European variety has 10 symmetrically arranged eye-spots (Nitsche, 1870 ; Calvét, 1900 ; Grave, 1930 ; Lynch, 1949).

BRACHIOPODA (LAMP-SHELLS), marine organisms of great antiquity which have existed unchanged since the Palæozoic era [1] and are found in the seas in most parts of the world covered by their shells firmly attached to rocks, are in some cases devoid of sense organs ; in the freely-swimming larvæ of others, patches of sensory epithelium form paired eye-spots immediately over the cerebral ganglion which disappear when the larvæ become sessile (*Cistella*) (Fig. 182) ; but rudimentary eyes are exceptional (*Megerlia*).



Brachiopod

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MOLLUSCA

Among MOLLUSCS (" soft bodied ") the most elementary types of eyes are found and also the most elaborate forms that the simple eye assumes, organs capable of a degree of resolution that the animal cannot probably utilize ; between the two extremes almost every imaginable form of eye is encountered. The characteristics of this phylum are an unsegmented body with a muscular " foot " protruding

[1] *Lingula*, with fossil records dating some 500,000,000 years, is the oldest known animal genus.

Solenogastre

from the ventral surface serving for locomotion, a dorsal or lateral fold of the body-wall to form a mantle or pallium within which lie the gills, and frequently a shell. As a general rule, two cephalic eyes subserve the visual function, but these may be replaced by more rudimentary organs in the dorsal region or around the margin of the mantle or at the end of the tentacles or the siphons. Occasionally eyes are lacking, in which case the skin has usually some sensitivity to light.

The large phylum of Molluscs is conveniently divided into six classes ; three are relatively unimportant, sluggish in habit, and live in the mud or sand of the sea-bottom—the shelled PLACOPHORANS and SCAPHOPODS, and the worm-like SOLENOGASTRES. The remaining three classes contain an enormous number of species of great variety—Gastropods, Lamellibranchs (Bivalves) and Cephalopods.

Nudibranch

The GASTROPODS (" belly-footed ") constitute a very varied group comprising some 40,000 species and include three main classes :

(*a*) OPISTHOBRANCHS : sea-hares, Pteropods (transparent marine plankton forms), and the brilliantly coloured Nudibranchs or sea-slugs which have no shell ;

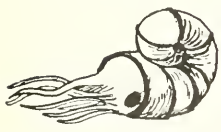
(*b*) PROSOBRANCHS, an enormous and varied group including sea-snails, whelks, limpets, Heteropods, etc. ;

(*c*) PULMONATES. The abundant and universally distributed fresh-water and terrestrial snails and slugs.

Pulmonate, *Limnæa*

The BIVALVES : shell-fish such as cockles, mussels, clams, scallops and oysters which live within a rigid hinged shell often at the bottom of the sea. They comprise some 11,000 species.

The remaining class, the CEPHALOPODS, are the most interesting ; they are usually active, moving by jet propulsion with a jet of water expelled from the siphon. Two orders are recognized : the Tetrabranchiates, with two pairs of gills, represented by a single living species, the Pearly Nautilus of the South Pacific, and the Dibranchiates, with a single pair of gills and remarkably well-developed eyes (cuttlefish, squid, octopus).



Nautilus

In the most primitive type of molluscs, the PLACOPHORANS, eyes may be lacking although some of their sensory organs may be sensitive to light (Plate, 1899 ; Nowikoff, 1907). Some of them possess a multitude of minute ocelli ; *Corephium*, for example, may have as many as 8,500. The most interesting in this class are the Chitons ("coats-of-mail") ; these possess cephalic eyes in the larval stage which, however, disappear as the adult becomes clothed by its eight-plated dorsal shell, thus rendering them useless. In [illegible] place numerous innervated papillæ appear conta[illegible] sensory organs (*æsthetes*) which perforate the sh[illegible]earing in rows as minute black dots (" shell-eye[illegible] Moseley, 1884) (Fig. 183). The larger of these

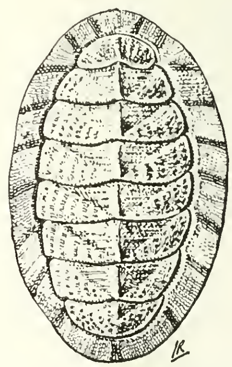


FIG. 183.—THE MOLLUSC, *CHITON*.

The sense organs, æsthetes, perforate the shell, appearing as minute black dots ; the larger of these contain an ocellus (Thomson's *Zoology*, James Ritchie ; Oxford University Press).

are light-sensitive, containing an ocellus composed of a deep retinal cup surrounded by pigment lying beneath a lens, the whole organ being covered by a cornea. It is to be remembered, however, that Crozier (1920) could find merely a general photosensitivity in *Chiton*, most pronounced where ocelli are lacking. Among SOLENOGASTRES, these organs are replaced by simple epithelial papillæ. In the SCAPHOPODA ("tusk-shells"), a small class of molluscs which burrow in the sand (*Dentalium*, elephant's-tooth shell, etc.) the sensory organs are represented only by statocysts.

Dentalium

Most members of the large class of GASTROPODS, the eyes of which were studied at an early date by J. Müller (1831), are provided with ocelli of a relatively primitive kind often associated with the tentacles. In the extremely passive limpet, *Patella*, the eyes at the base of the tentacles are very elementary, being merely represented by simple

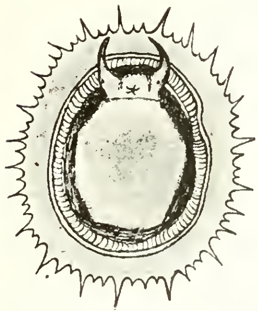


FIG. 184.—THE LIMPET, *PATELLA VULGATA*

Ventral surface. Note the simple eyes (appearing as black dots) at the base of the 2 tentacles. The star-shaped median structure is the mouth (Thomson's *Zoology*, James Ritchie ; Oxford University Press).

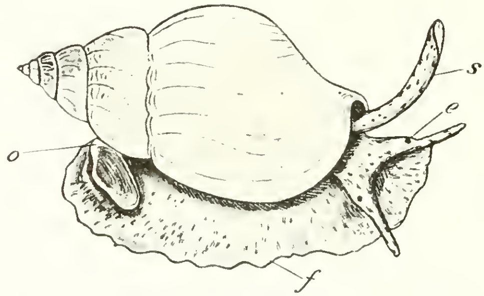
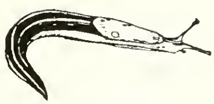


FIG. 185.—THE COMMON WHELK OR BUCKIE, *BUCCINUM UNDATUM*.

Note the two simple eyes (*e*) at the base of the tentacles. *s*, respiratory siphon ; *o*, operculum ; *f*, foot (Thomson's *Zoology*, James Ritchie ; Oxford University Press).

cupulate depressions of sensory and pigmented cells (Figs. 97 and 184). More usually, however, the eyes are vesicular in type. These are typified in the two simple vesicular eyes of the grey slug, *Limax*, or the snail, *Helix* (Fig. 110), perched on the tips of the two longer (and posterior) tentacles ("horns") and innervated from the cerebral ganglion (Galati-Mosella, 1915) ; on exposure to light the tentacle is capable of retraction like the finger of a glove so that the eye can be drawn within it (Figs. 186 to 188). The common whelk, *Buccinum*, has eyes of a somewhat similar vesicular type situated near the base of the tentacles (Fig. 185), as also has *Murex*.



Limax

Shell of *Murex*

The most elaborate eye of this type, however, is seen in the spider-shell, *Pterocera lambis*, a gastropod found in quantity on tropical reefs. According to

Figs. 186 to 188.—The Common Garden Snail, *Helix aspersa.*

Fig. 186.—The two eyes are situated on the tip of each of the long posterior horns.

Fig. 187—The eye at the tip of the expanded horn.

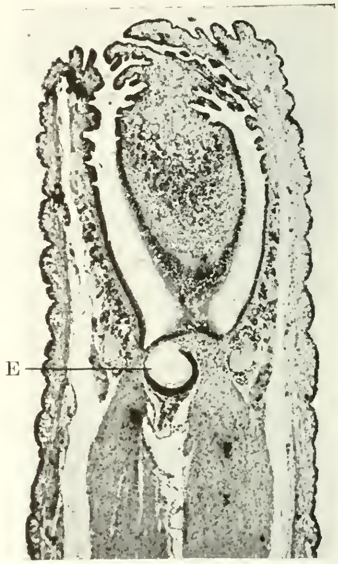


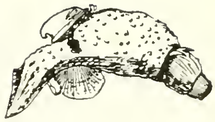
Fig. 188.—The eye (E) retracted into the horn. The horn invaginates like the inturned finger of a glove ; the obliquity of this section gives the appearance of a double cavity (Norman Ashton).

Shell of *Pterocera*

Prince (1955), the two vesicular eyes, which have an elaborate neural structure,[1] are mounted on the tip of stalks (ommatophores) which also carry an olfactory tentacle and a sensory node (Fig. 189). These, supplied with muscles arranged round a central sinus, are retractile partly by muscular activity and partly by fluid engorgement by hæmolymph. Retraction can be slow and voluntary or l and reflex in response to stimuli such as touch, odour or the cutting off of ; the reaction is thus the opposite of that seen in the snail. It appears al at a certain amount of convergence upon an object is possible.

[1] p. 142.

In *Onchidium*, a naked littoral Pulmonate which creeps on rocks near the high-water mark, a unique type of vesicular eye with an inverted retina is found arranged on papillæ scattered over the skin of the back in groups of six or up to a total which may reach a hundred (Fig. 122).[1]



Carinaria

An interesting elaboration is seen in some marine HETEROPODS (*Carinaria*,

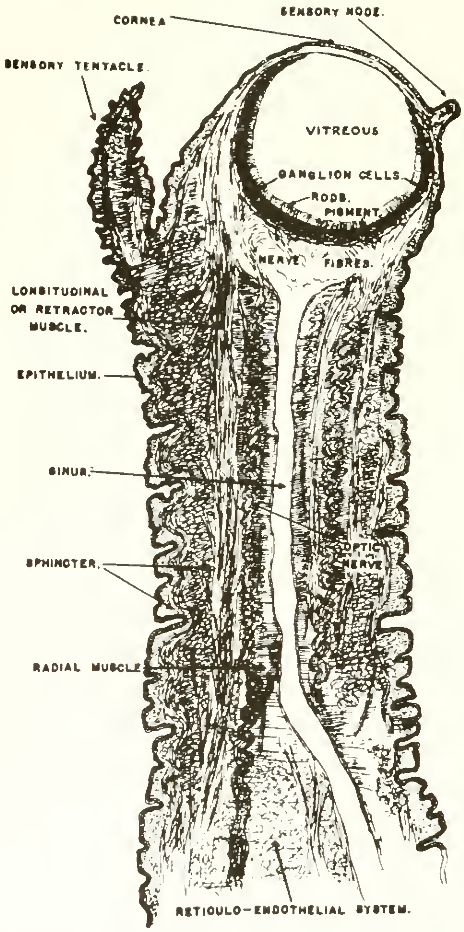


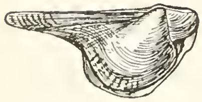
FIG. 189.—THE STALKED EYE OF THE SPIDER-SHELL, *PTEROCERA LAMBIS*.

Showing the sensory tentacle, sensory node, sinus, and muscular systems (after J. H. Prince).

Pterotrachea) which have tubular eyes containing a large spherical lens; the available visual field is increased by the provision of lateral " windows " wherein pigment is lacking, opposite which the posterior retina is prolonged up the side of the eye. *Pterotrachea coronata* which swims with its belly in the air has an eye at the extremity of each of its two tentacles ; images in front are focused on the posterior retina by the enormous lens, while movements and changes in

[1] p. 148.

illumination above and below are probably appreciated through the dorsal and ventral " windows " (Hesse, 1908 ; v. Hess and Gerwerzhagen, 1914). Such fenestrated eyes are also seen in abyssal fishes.[1]



Avicula

LAMELLIBRANCHS OR BIVALVES have an undeveloped head-region, and the two lobes of the mantle which secrete the two valves of the shell are frequently united posteriorly to form exhalant and inhalant siphons. Anterior eyes are therefore rare. Such cephalic eyes are sometimes seen in larval forms but in the adult they tend to become vestigial remnants, a cupulate depression of bipolar sensory and

Mytilus

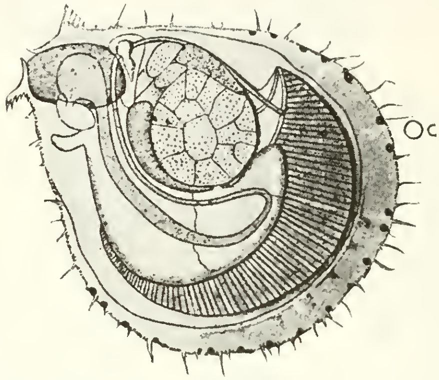


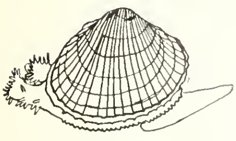
FIG. 190.—THE COMMON SCALLOP, *PECTEN*.

The pallial ocelli, Oc, are seen in a single row round the margin of the mantle. For section of the eye, see Fig. 123 (after Pelseneer).

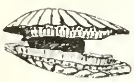
pigmented cells as occurs in the pearl-oyster, *Avicula*, or the edible mussel, *Mytilus*. More usually they are replaced by ocelli located in situations where they are of greater biological value such as the siphons, the tentacles or the mantle (Fig. 190).

Pholas

Thus the ocelli are found on the inner surface of the siphons in clams which habitually lie buried in the sand or mud (*Mya*) or bore into soft rocks (*Pholas*) (Light, 1930) ; as they lie buried these molluscs extend the siphon to the surface to feed and at daybreak or whenever the illumination increases the siphon is withdrawn (Wenrich, 1916 ; Hecht, 1919–20 ; Piéron, 1925 ; Folger, 1927 ; and others). It will be remembered that these visual organs are of the most simple type resembling those of the earthworm, being merely single cells of the apolar type with a refractive organelle in the cell-body richly supplied with nerves.[2] In the cockle, *Cardium*, small ocelli are situated at the tips of the tentacles, about 100 in number, which are arranged around the siphonal apertures ; the eye is of a simple cupulate form, the cup-shaped retinal cells resting on a layer of double pigmented cells underneath a large ectodermal cell for lens and cornea (Kishinouye, 1894). As in the pallial eyes of *Pecten*, the retina is inverted.



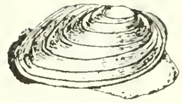
Cardium



Pecten

[1] p. 323. [2] p. 131.

Most bivalves, however, have numerous ocelli arranged like a coronet around the margin of the mantle (PALLIAL EYES) ; these may be numbered in hundreds and are probably to be looked upon as modified tentacles. In some forms, such as *Lima*, they are very primitive. This bivalve is provided with 30 simple cup-shaped depressions, 0·3 mm. in diameter, lined with sensory and pigmented cells forming primitive cupulate eyes ; in others such as the fresh-water mussel, *Anodonta*, eyes are completely absent. Most of these types are relatively sluggish and quiescent, but in actively swimming forms the eyes may be more elaborate. This development is well exemplified in such bivalves as the common scallop, *Pecten*, and *Spondylus*, both of which possess eyes unique among Molluscs. The pallial eyes are arranged in a single row around the edge of the mantle ; when they are exposed as the shell gapes they shine as brilliant emerald green or purple spots, 0·6 to 0·8 mm. in diameter ; 28 to 46 have been counted in the upper half of the mantle, 15 to 36 in the lower, and each is borne on a contractile pedicle (Fig. 190). These are of remarkable complexity with a well-formed inverted retina which appears to be much more elaborate than the visual demands of the shell-fish would seem to warrant (Fig. 123). Each is connected by means of its optic nerve with a large circumpallial nerve and so with the branchial ganglion.[1] An anomalous occurrence in certain lamellibranch molluscs (the Noah's-ark shell, *Arca* ; *Pectunculus*), is that of unicellular ocelli grouped together in a spherical mass constituting an aggregate eye which bears a superficial resemblance to a compound eye [2] (Carrière, 1885 ; Patten, 1886 ; Hesse, 1900).



Anodonta

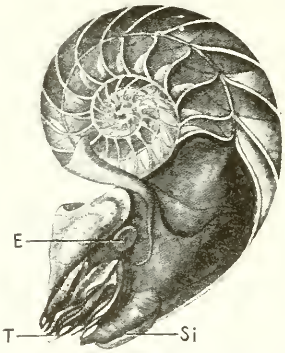


FIG. 191. — THE PEARLY NAUTILUS, *NAUTILUS POMPILIUS*.

The animal is seen in section. Above is the spiral shell. E, the eye, which opens to the exterior ; Si, siphon ; T, tentacles (after Owen).

The CEPHALOPODS (cuttlefish, etc.) usually exhibit the most elaborate visual organs found among Molluscs, a characteristic understandable in view of their active behaviour and carnivorous habits ; only one species living at abyssal ocean depths is known to lack eyes, *Cirrothauma murrayi*.[3] They are the most specialized of the molluscs and present considerable diversities of type, but most of them are freely swimming and they all have a well-developed head furnished with numerous "arms" bearing tentacles or suckers and provided with eyes and other sensory structures.

Spondylus

In the pearly nautilus of the seas of the Far East, the sole survivor of the primitive and almost extinct tetrabranchiate Cephalopods which were largely Palæozoic in distribution, the eye retains its ancestral simplicity and consists merely of an epithelial depression with a tiny aperture 2 mm. in diameter (Figs. 100 and 191) ; it is situated on a raised flat peduncle which is also provided with two "ocular tentacles", probably olfactory in function.

Sepia

In the more recent and voraciously carnivorous dibranchiate Cephalopods, however, such as the common cuttlefish, *Sepia*, the

[1] p. 527. [2] p. 151. [3] p. 723.

squid, *Loligo,* and the octopus, the two eyes are large and prominent (Figs. 192–3). They are situated conspicuously on either side of the head behind the main body of tentacles, protected in part by the cartilage surrounding the brain and in part by cartilages in their own

Fig. 192.—*Octopus vulgaris* (J. Z. Young).

walls, and provided with rudimentary lids and a set of 4 extra-ocular muscles which confer a wide range of movement on the globe (Hesse, 1908 ; Tompsett, 1939) (Figs. 113 and 114). The complex structure of these organs has already been described,[1] and although they rival the eyes of Vertebrates in their morphology, they are simple in type, derived from the epithelium. The close resemblance of the eyes of these molluscs to the cerebral "camera" eyes of Vertebrates is a striking example of convergent evolution whereby Nature achieves comparable results by travelling along entirely different routes. The nervous connections are prominent ; in the posterior wall of each eye is a large optic ganglion from which the thick optic lobes lead directly to the closely associated cerebral ganglion [2] (Fig. 698). There is a well-developed olfactory sac behind each eye as well as two statocysts and organs of general sensation, but it would seem that vision plays a dominant part in the behaviour of the animal.[3]

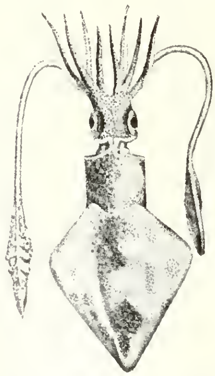


Fig. 193.—The Common Squid, *Loligo vulgaris.*

Showing the two large prominent eyes, one on each side of the head (after K[illegible]in).

[1] p. 143. [2] p. 528. [3] p. 575.

Anomalous types of eyes are seen among Cephalopods found at great ocean depths (Chun, 1903). Stalked eyes comparable to those found in some deep-sea fishes, are exemplified in *Bathothauma* (Fig. 194) and *Sandalops* (Fig. 195); both of these live at great depths in the South Atlantic and the eyes of the latter are unique in that they point obliquely downwards, a curious configuration said to be explained by the fact that the squid swims with its body slanting upwards.

FIGS. 194 TO 196.—THE EYES OF DEEP-SEA CEPHALOPODS.

FIG. 194.

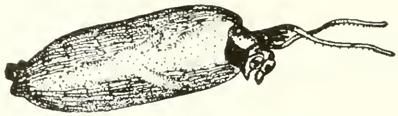


FIG. 195.

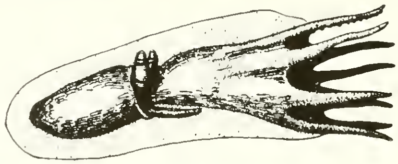


FIG. 196.

FIG. 194.—The deep-sea squid, *Bathothauma*. There are luminous organs beside the eyes which are perched on the end of stalks. Found at a depth of 3,000 m. (from the *Valdivia* Reports).

FIG. 195.—The deep-sea squid, *Sandalops melancholicus*. The stalked eyes are unique in that they point obliquely downwards, possibly because the animal swims with its body slanting upward (from the *Valdivia* Reports).

FIG. 196.—The pelagic octopus, *Amphitretus*. The tubular eyes point upwards and the whole body, including the eyes, is covered with a delicate gelatinous covering (from the *Valdivia* Reports).

Another curious arrangement is seen in *Amphitretus* (Fig. 196) found in the Indian and Pacific oceans. The eyes of this octopod resemble the tubular organs of some deep-sea fishes,[1] pointing directly upwards and enclosed, as is the entire body of the animal, in a delicate and transparent gelatinous covering.

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[1] p. 322.

ARTHROPODA

ARTHROPODS embrace more than three-quarters of the known species of animals, and in view of their number and variety and the diversity of their habits, it is not surprising that an extraordinary variation occurs in their visual organs, while the intense and purposive activity of many of them accounts for the complexity and efficiency of their eyes. Arthropods are characterized by their bilateral symmetry, their segmental structure with jointed appendages, their chitinous cuticle, a distinct head where the sense organs are aggregated, and a nervous system consisting of a dorsal brain-ganglion connected by a ring round the gullet with a double chain of ventral ganglia. From the ocular point of view, although simple eyes often of quite a rudimentary type are frequent, and may indeed be the sole visual organs (as in Arachnids), the characteristic feature of the phylum is the presence of compound eyes of elaborate structure and frequently with highly developed functional abilities.

The Arthropods may conveniently be divided into five sub-phyla :

(1) the primitive worm-like ONYCHOPHORA, unique in having a soft, velvety skin, and provided with a separate head, one pair of antennæ and 20 legs all alike ;

(2) the CRUSTACEANS, comprising some 25,000 species, with the head fused with the thorax, 2 pairs of antennæ and at least 5 dissimilar pairs of legs ;

(3) the MYRIAPODS (centipedes, millipedes, etc.), of some 2,000 species, with a distinct head, one pair of antennæ and numerous legs all alike ;

(4) the ARACHNIDS, of some 36,000 species, having 2 body-segments with a fused cephalothorax, without antennæ or wings, and 4 pairs of legs ;

(5) the INSECTS, of which more than 577,000 species have now been scientifically described and probably several times as many await investigation, with a body divided sharply into 3 segments, head, thorax and abdomen, bearing one pair of antennæ, 3 pairs of legs and (usually) one or two pairs of wings in the adult.[1]

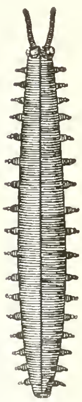


FIG. 197. — THE ONYCHOPHORE, *PERIPATUS*.

Note the two simple eyes on top of the head at the base of the antennæ (Thomson's *Zoology*, James Ritchie ; Oxford University Press).

ONYCHOPHORA

The most primitive class of Arthropods, the ONYCHOPHORA (*Peripatus* and its allies), inhabiting the forests of the Southern Hemisphere, represent an archaic type, differing widely from other members of the phylum. Seeking out damp places under leaves

[1] In one acre of farm-land in England it has been estimated that there are from 700,000,000 to 800,000,000 Insects and as many Arachnids. They would usurp Man's domination of the earth were their numbers not kept in check by voracious predators and parasites of their own kind.

and in rotting wood, they are shy and nocturnal in habit with a marked dislike of light. They are beautiful, velvety, caterpillar-like creatures with paired eyes set like diamonds (0·2 to 0·3 mm.) on the side of the head behind the two sensitive antennæ, looking upwards and outwards, not forwards (Fig. 197) ; the eyes, like those of marine Polychætes, are of

Figs. 198 to 200.—The Eyes of the Large Crustaceans (Decapods) (Specimens from Natural History Museum, London).

Fig. 199.

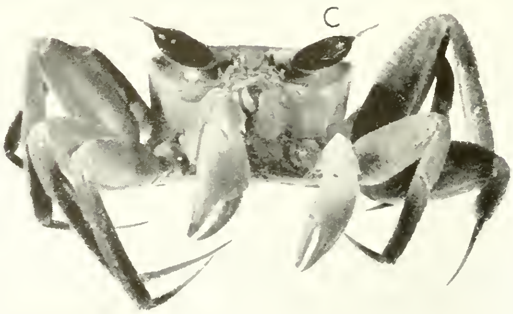


Fig. 198.

Fig. 200.

Fig. 198.—The common shrimp, *Crangon vulgaris*. The short eye-stalks bearing the compound eyes lie in sockets in the carapace.

Fig. 199.—The fiddler crab, *Gelasimus arcuatus*. There are two compound eyes, C, each standing out prominently on a muscular eye-stalk and protruding on either side of the median rostrum. The left claw is represented by a small stump ; the huge right claw gives the animal its name.

Fig. 200.—The racing crab, *Ocydpoda ippens*. Two prominent elongated compound eyes, C, are set on eye-stalks, in sockets on the carapace.

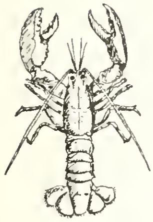
the simple type, cupulate in form with a corneal lens formed by the cuticle and hypodermal cells (Fig. 103). Eyes so simple as this serve merely as a means of orientation away from light, and two cave-dwelling species are blind [1] (Dakin, 1921).

CRUSTACEA

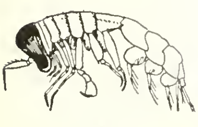
The CRUSTACEANS (lobsters, crabs, shrimps, water-fleas, barnacles, etc.) with few exceptions (land-crabs, wood-lice, sand-hoppers) are aquatic in habit and in most the eyes are prominent ; some pelagic forms are transparent except for the eyes which are highly coloured or phosphorescent. Compound eyes are usually present, occasionally supplemented by eyes of the simple type, but in sessile or parasitic forms the visual organs may be vestigial or lacking. Most forms

FIG. 201.—THE WOODLOUSE, *Sphæroma lanceolata*.

The compound eyes, C, are sessile, lying on the extreme lateral aspects of the head segment (specimen from Natural History Museum, London).



Homarus



Phronima

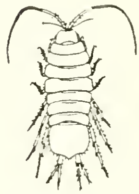
commence life as a nauplius larva with an oval body, three pairs of limbs and a single eye in the middle of the head.

Of the larger forms (the sub-class MALACOSTRACA) the Decapods (lobsters, shrimps, prawns, crabs) have the most elaborate eyes ; of these the common lobster, *Homarus vulgaris*, may be taken as representative. It possesses two typical compound eyes, each with a multitude of ommatidia, associated with the procephalic lobes of the cerebral ganglion. They stand out prominently on muscular eye-stalks to protrude on either side of the median rostrum and are capable of some degree of movement (Fig. 198). In crabs a similar pair of compound eyes with relatively few but large ommatidia are set on eye-stalks in sockets in the carapace (Figs. 199–200). The fact that the eye-stalks [illegible] in the crab and in the crayfish exhibit optomotor reactions as when [illegible]imal turns or is confronted by a black and white striped rotating d[illegible] indicates that their movements are optically determined

[1] p. 724.

(v. Buddenbrock *et al.*, 1954 ; Dijkgraaf, 1956). One group, the Eryonidea, confined to the deep seas, are blind, the eyes being reduced to stalks only. In other species the eyes are sessile, both in terrestrial Isopods (such as woodlice, Fig. 201) and in pelagic Amphipods : among the latter in the smaller forms the eyes may be minute (*Caprella*, Fig. 202), while in the larger forms they may assume enormous dimensions (the "wondrous-eyed hopper," *Thaumatops magna*, Fig. 203). Sedentary types such as *Asellus*, an Isopod which lives in holes, are completely blind.

Euphausiid Crustacean



Asellus

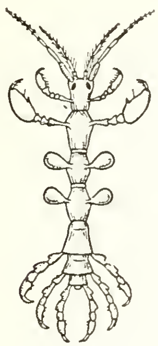


FIG. 202.—THE AMPHIPOD, *CAPRELLA LINEARIS*.

Two ocelli are seen on the dorsal surface of the head.

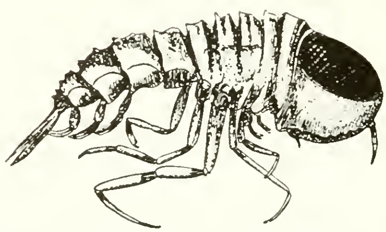


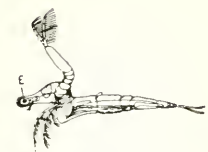
FIG. 203.—THE "WONDROUS-EYED HOPPER," *THAUMATOPS MAGNA*.

The largest known hyperiid Crustacean, found at a depth of 2,500 m., with enormous compound eyes (to the right) (¾ natural size) (after Brehm).

The smaller Crustaceans (branchiopods, copepods, ostracods, cirripedes) include a vast number of types in which the active swimming forms are provided with eyes, while in most sessile and parasitic forms the organs become degenerate. They comprise four diverse and little related orders :

Artemia

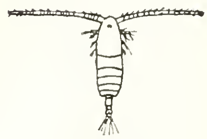
(*a*) BRANCHIOPODS—protected by a shell and provided with 4 pairs of leaf-like swimming feet. They comprise two groups : (1) the PHYLLOPODA such as the brine-shrimp, *Artemia*, which can survive even in Salt Lake, and the large fresh-water *Apus*, of world-wide distribution, and (2) the laterally compressed minute water-fleas (CLADOCERA), *Daphnia*, *Polyphemus* and *Leptodora*, so abundant in fresh water.



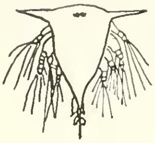
Leptodora

(*b*) OSTRACODS—small laterally compressed creatures with a bivalve shell and indistinct segmentation, breeding parthenogenetically. Typical examples are the fresh-water *Cypris* and the salt-water *Cypridina*.

(*c*) COPEPODS—elongated segmented creatures without a protective shell. Typical examples are the beautiful fresh-water *Cyclops* and the salt-water *Calanus*. Copepods occur in vast numbers in the seas and constitute the most



Calanus



Nauplius larva

abundant animal constituent of the plankton. The group also contains some parasites, as the common fish-louse, *Caligus*.

(*d*) CIRRIPEDES—with an indistinctly segmented body and usually provided with a calcareous shell. They have a complex life-history. They are born as actively swimming nauplius larvæ, develop into a pupal cypris-like stage, again swimming freely with appendages, but in the adult condition lead an entirely sessile or parasitic life. Typical examples are the barnacle, *Lepas*, which attaches itself to the bottoms of ships or floating logs, the acorn-shell, *Balanus*, which

FIGS. 204 TO 206.—THE EYES OF SMALL CRUSTACEANS (Specimens from Natural History Museum, London).

FIG. 204.

FIG. 205.

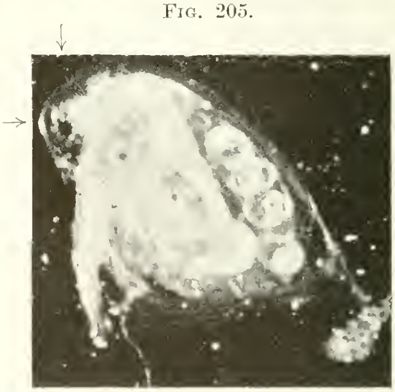


FIG. 206.

FIG. 204.—The dorsal surface of a Branchiopod, *Triops* (*Apus*) *cancriformis*. In the anterior region are two compound eyes, C, and behind them a median eye of the composite simple type, S.

FIG. 205.—An Ostracod, *Cypria ophthalmica*. The single deeply pigmented eye, E, is seen shining through the semi-transparent shell.

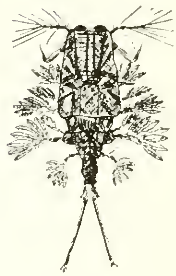
FIG. 206.—The water-flea, *Daphnia*. Prominently in the head region (at the junction of the arrows) is the compound eye, appearing as a mass of pigment with little facets round it. Behind and underneath lies the minute composite median eye (see also Fig. 145).

encrusts the rocks between tidal marks in enormous numbers, and *Sacculina*, one of the most degenerate of parasites which becomes an endoparasite in the abdomen of crabs.

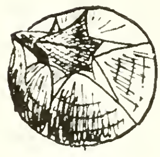
The characteristic ocular feature of the whole group is the presence of a median unpaired eye ; it is sometimes unique, as in *Cyclops*, sometimes associated with a single compound eye, as in *Daphnia*, sometimes with paired lateral eyes which may be either simple, as in *Pontellopsis*, or compound in type, as in the Phyllopod, *Apus* (Fig. 204). In *Apus* the median eye is really a paired organ but the two are so closely situated that they appear on examination to be a single spot. The median eye of these small Crustaceans is situated either dorsal or ventral to the cervical ganglion and is of the composite simple type[1]; it is composed of the fusion of a number of constituent ocelli (usually 3). Such a median eye is present in most of the Branchiopods and Ostracods, only occasionally degenerating when the compound eyes are particularly well developed (*Polyphemus*, *Leptodora*).


Polyphemus

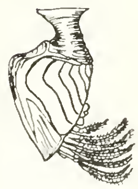
The ocular arrangements in these actively swimming small Crustaceans is therefore very varied. The eyes of the water-flea, *Daphnia*, may be taken as representative of the Branchiopods and Ostracods. There is a single compound eye in the mid-line composed of 22 relatively rudimentary ommatidia (Fig. 206). Behind and below this, buried in the central nervous system, is the small composite ocellus (Figs. 131 and 145). It is interesting that the compound eye is actively motile, being kept in a state of continual vibration by 4 muscles somewhat resembling in their arrangement the rectus muscles of vertebrates (Rabl, 1901 ; Hess, 1912). It would seem that the small composite ocellus is of little functional value. The phototactic responses exhibited by the animal depend entirely upon the more elaborate compound eye ; when this has been removed the phototactic responses fail although the more primitive generalized sensitivity to light persists (Schulz, 1928 ; Harris and Mason, 1956).


Copilia

The eyes of some of the actively swimming Copepods take on another form. In the female *Pontellopsis regalis*, there are two very small dorsal ocelli symmetrically placed and a large unpaired median eye situated fronto-ventrally underneath the rostrum ; it has a large cuticular lens and 6 retinal cells arranged in an inverted position in two groups of 3, forming an intermediate step between a simple eye and an ommatidium (Vaissière, 1954–55). The elongated, actively motile eyes of *Copilia* are of the same general structure with a retinule of 3 sensory cells (Fig. 139) (Grenacher, 1880–95 ; Exner, 1891). This animal has two such eyes facing forwards and widely separated ; in *Sapphirina* they are close together ; and in *Corycæus* so close that the lenses are fused in the mid-line.


Balanus

In sessile forms eyes are usually present in the actively swimming nauplius stage ; thus in the acorn-shell, *Balanus*, there is initially a median unpaired eye but after several moults in the pupal stage two lateral composite eyes are acquired. In adult life, however, these become vestigial, as also does the unpaired eye of the ship-barnacle, *Lepas* (Fales, 1928). In some parasitic forms such as the fish-louse, *Caligus*, both median (simple) and lateral (composite) eyes are also present, but in degenerate types such as *Sacculina* eyes and other sense organs are lost.


Lepas

[1] p. 152.

MYRIAPODA

The MYRIAPODS (the quick-moving, carnivorous solitary centipedes or Chilopoda, some with more, some with less than 100 legs, and the slow-moving vegetarian, gregarious millipedes or Diplopoda) are characterized by the possession of two groups of ocelli forming aggregate eyes on either side of the head so closely packed together as to suggest a compound eye (Figs. 207 to 210); so close are they in the Chilopod, *Scutigera*, that they form a pair of true compound eyes (Grenacher,

FIGS. 207 TO 210.—THE AGGREGATE EYES OF MYRIAPODS (Specimens from Natural History Museum, London).

FIG. 207.

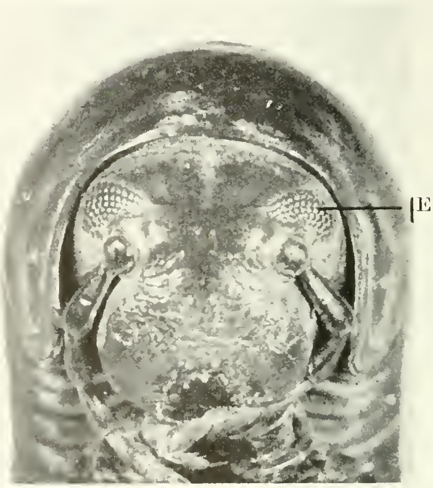


FIG. 208.

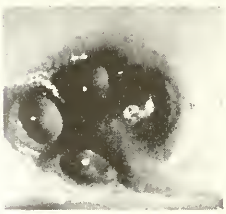


FIG. 209.

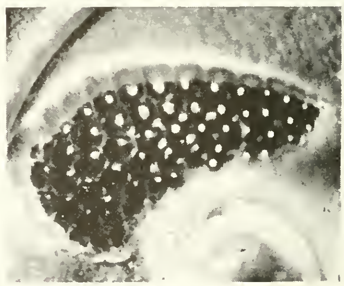


FIG. 210.

FIGS. 207 AND 209.—The centipede, *Scolopendra morsitans* from India. The group of 4 ocelli, E, are situated on either side of the head.

FIGS. 208 AND 210.—A Spirostreptid millipede from the Seychelles. The group of ocelli forming an aggregate eye, E, is seen on either side above the antennæ. Fig. 210 shows the close resemblance to a true compound eye.

1880; Graber, 1880; Caesar, 1913; Constantineanu, 1930). In some types, such as *Pauropus*, which live in moist debris in the woods and forests, eyes are lacking.

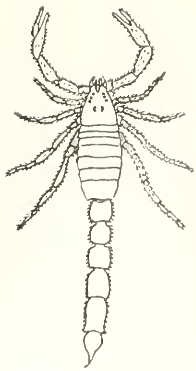
ARACHNIDA

The ARACHNIDS form a large and loosely associated group which includes scorpions, king-crabs, spiders, pseudo-scorpions, whip-tailed scorpions, harvest-men, jerrymanders, mites and ticks. With the single exception of the king-crab they do not possess compound eyes

FIG. 211.—THE KING-CRAB, *LIMULUS POLYPHEMUS*.

A simple eye, S, is seen as a dark spot situated on either side of the median spine. The two compound eyes, C, are situated on the external aspect of each of the first lateral spines (specimen from Natural History Museum, London).

but all are provided with ocelli sometimes of considerable size and complexity.



Scorpion

SCORPIONS (SCORPIONIDEA), venomous animals up to 8 in. in length with a long stinging tail, are restricted to warm countries; in habit they are essentially solitary and nocturnal, being active during the night and spending the day lurking under stones or in crevices. They are provided with a pair of large median eyes situated about the middle of the cephalothorax, and 2 to 6 pairs of lateral ocelli placed on its antero-lateral margins, the more anterior being simpler in structure than the posterior.[1] The lateral eyes are simple ocelli in which the

[1] p. 141.

borders of the visual cells unite with their neighbours to form rhabdomes (Fig. 109); the median eyes are also of the simple type with the sensory cells arranged in groups each centred on a rhabdome. These cells, however, are peculiar in that they are doubled upon themselves to form a semi-inverted retina [1] (compare Fig. 127).[2]

The KING-CRABS (XIPHOSURA), a very ancient type dating to the Silurian, which live in shallow water on the sandy shores of North America (*Limulus*) or Asia, have two large lateral compound eyes and two median ocelli (Fig. 211). The compound eye is of a unique and elementary type [3] (Fig. 143); it is not faceted but is covered by a chitinous thickening of the cuticle which sends projections inwards as

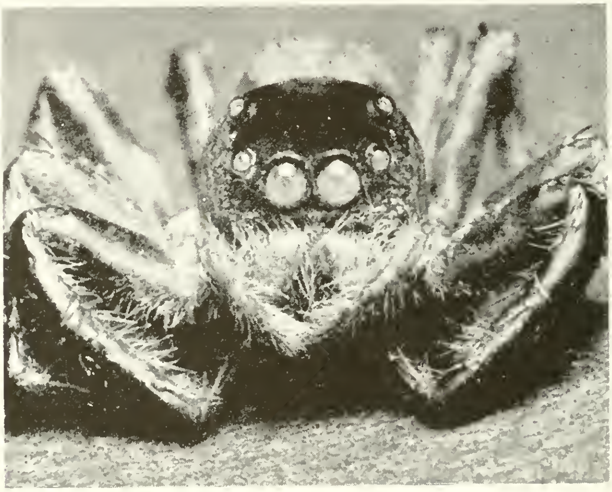


FIG. 212.—THE JUMPING SPIDER, *PLEXIPPUS SINUATUS*.

From the Dutch East Indies. The 2 large and 6 small simple eyes are seen surrounding the anterior and lateral aspects of the carapace (specimen from Natural History Museum, London).

conical papillæ over each ommatidium to form a corneal lens. The small median eyes are of the simple type wherein the sensory cells are associated with rhabdomes (Fig. 142).

In addition, a third pair of ventral eyes is present in the larva on either side of the frontal organ of the hypostoma, an olfactory organ; in the adult these eyes become degenerate but it is possible that they may participate in the olfactory function (Patten, 1893; Hanström, 1926).

[1] ... 0.

[2] ...etails, see J. Müller (1826), Lankester and Bourne (1883), Parker (1887), Petrun... (1907), Police (1908), Scheuring (1913–14), Bütschli (1921), Versluys and De... 1923).

[3] p.

SPIDERS (ARANEIDA) are of widespread distribution and, although comprising some 14,000 species, are conveniently divided according to their habits into two types, the relatively sedentary "web-spinners" and the more active "wanderers" which hunt their prey; all, however, spin silk, either as a web, or for snaring or tying up their victims, for protection of their cocoons or for making bridges for travelling. In both types on the cephalothorax there are 6 or more usually 8 simple eyes arranged in two or three rows (Fig. 212); these have received a considerable amount of study.[1] The arrangement of these ocelli varies remarkably (Figs. 213 to 216). Among the web-spinners the ocelli are rudimentary and their effective range is short. The common house

FIGS. 213 TO 216.—THE ARRANGEMENT OF THE OCELLI IN DIFFERENT SPECIES OF SPIDERS.

FIG. 213.—The ocelli of the common house spider, *Tegenaria domestica*.

FIG. 214.—The ocelli of the common garden spider, *Araneus diadematus*.

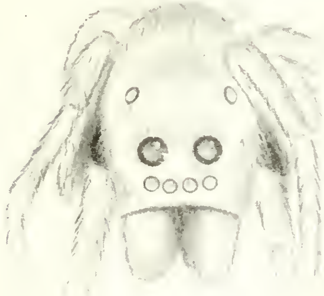
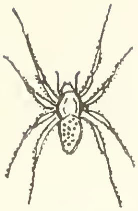


FIG. 215.—The ocelli of the wolf spider, *Lycosa agricola*.

FIG. 216.—The ocelli of the jumping spider, *Salticus scenicus*.

[1] For details, see Hentschel (1899), Widmann (1908), Petrunkevitch (1911), Scheuring (1914), Versluys and Demoll (1923), Savory (1928), Homann (1928–53), Millot (1949).


Tegenaria

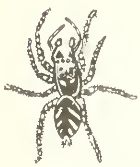

Araneus

spider, *Tegenaria domestica*, has two rows of 4 ocelli, those of the anterior row being slightly smaller than those of the posterior (Fig. 213); the common garden spider, *Araneus diadematus*, has 4 median and 4 small lateral eyes (Fig. 214). The more active hunting species which construct no web have larger eyes ; thus the wolf-spider, *Lycosa*, has an anterior row of 4 small ocelli, two large posterior median and two smaller posterior lateral ocelli (Fig. 215) ; while the jumping-spider, *Salticus*, with a visual capacity more fully developed than the wolf-spider, has an anterior row of two large and two smaller ocelli on the front of its square-shaped cephalothorax, and two very small posterior median and two posterior lateral ocelli on the top (Fig. 216). With all its variations the general plan is thus consistent ; the anterior median eyes (the two central eyes in the front row) have a verted retina, the remainder are inverted provided with a crystalline tapetum [1] and since these latter glow in the dark the former are sometimes called " diurnal eyes." The nerve-fibres from the two anterior median eyes travel—with a partial decussation at a chiasma—to the ganglion of the first cephalic segment, from the remaining eyes to that of the second (Figs. 107, 126).


Lycosa

It is interesting that the anterior median eyes of spiders are equipped with muscles attached to their posterior aspect rendering them motile so that they can increase their visual field ; thus web-spiders have one muscle, Lycosids two, and Salticids six. These are absent in the lateral and posterior median eyes.

Curious anomalies to this general arrangement exist, but they are rare ; thus in the female of a spider found in France, *Walckenaera acuminata*, the eyes are arranged on a dumpy tubercle on the cephalothorax, while in the male they are perched on a long stalk-like periscope, 4 on the tip and 4 half-way down (Millot, 1949). It is interesting that among spiders the lens, which is part of the outside covering of the animal, is cast at the time of moulting and thus it would appear that the spider may be rendered temporarily blind.


Salticus

PSEUDO-SCORPIONS (PSEUDOSCORPIONIDEA), minute animals resembling miniature scorpions but without the long tail and sting, found burrowing in books or under stones, the bark of trees and the wing-covers of insects, are provided with two pairs of simple eyes (when they exist) on either side of the cephalothorax ; these are typically equipped with an inverted retina and a tapetum (Scheuring, 1913) (Fig. 217).


Whip-scorpion

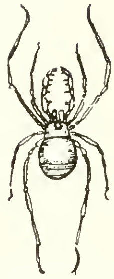
WHIP-TAILED SCORPIONS (PEDIPALPI). The eyes of this order are not well known (Scheuring, 1913 ; Versluys and Demoll, 1923 ; Millot, 1949). They are entirely absent in some species ; in others there are two median eyes only ; but the typical arrangement consists of two median (principal) eyes and two groups of 3 lateral eyes.

[1] Except *Salticus*, the eyes of which lack a tapetum and are therefore " diurnal ". See p. 150.

The median eyes are of the cupulate type with a semi-inverted retina the cells of which are doubled upon themselves [1] (Fig. 127). The lateral eyes have an inverted retina with a tapetum (Fig. 124).

Fig. 217.—The Pseudoscorpion, *Chthonius ischnochules*.
Showing two simple eyes, S, on either side (specimen from Natural History Museum).

harvestmen (phalangida ; opiliones), minute spider-like Arachnids with extremely long legs, which avoid the glare of daylight, have two simple ocelli mounted one on either side of an oculiferous tubercle (ocularium) (Fig. 218). It would seem that with its laterally directed eyes the animal has no frontal vision. Each ocellus is a simple



Harvestman

Fig. 218.—The Eye of the Harvestman, *Megabunus diadema*.
The simple eye is seen on a special oculiferous tubercle (specimen from Natural History Museum).

cupulate eye with a large cuticular lens and a simple row of visual cells from which the fibres emerge in several branches to form the optic nerve (Purcell, 1894).

[1] p. 150.


Jerrymander

JERRYMANDERS (SOLIFUGÆ)—active, pugnacious, non-venomous, nocturnal creatures found in warm countries—possess a pair of median (principal) eyes situated on a small tubercle and one or two pairs of lateral eyes usually rudimentary, difficult to see and probably functionless. Both types are simple cupulate ocelli with direct (verted) retinæ (Scheuring, 1913; Demoll, 1917).

MITES and TICKS (ACARINA). MITES are minute Arachnids of which over 20,000 species are known, found almost universally in the earth or in water, salt and fresh, often of parasitic habit on or within animals (including man) and plants whether alive or decaying after death: well-known human parasites are *Sarcoptes scabiei* (the itch-mite) causing scabies, and *Demodex folliculorum* found in the hair follicles; the harvest-mite (chigger) is a virulent pest to both man and animals (particularly rodents), while others infest insects (Isle of Wight bee disease) and others plants (gall mites, red spiders, etc.). Many, such as *Sarcoptes* are without eyes (Fig. 219); others, such as the Prostigmata and the Hydracarina (fresh-water mites) are provided with 2, 4 or 6 ocelli on the front and lateral aspects of the head depending on the species, the individual organs being sometimes fused (Fig. 220 and 221) (Lang, 1905). Each possesses a convex lens often difficult to distinguish from the surrounding skin.

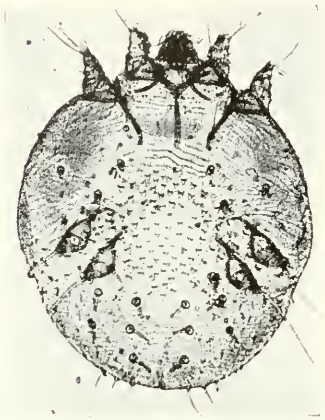


FIG. 219.—THE MITE, *SARCOPTES SCABIEI*.

(Female) (× 125) (Sutton and Sutton, *Hb. of Dis. of the Skin*, Mosby).

TICKS (IXODIDES) are larger than mites and are frequently of biological importance as causing disease (tick-fevers) in man[1] and animals.[2] Most types are without eyes, but such species may have thin transparent areas on the dorsal surface which perhaps respond to differences in the intensity of light. When visual organs are present they are extremely rudimentary, being minute ocelli mounted curiously on the animal's shoulder (Fig. 222).

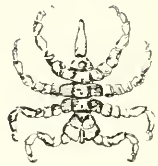
FIGS. 220 AND 221.—THE EYES OF FRESH-WATER MITES (HYDRACARINA).


FIG. 220.—The 4 separate ocelli of *Limnesia*.


FIG. 221.—*Hygrobates*, showing fusion of the anterior and posterior ocelli (after P. Lang).

[1] Texas fever, Rocky Mountain spotted fever, etc.
[2] Red-water fever in cattle, heart-water in sheep, etc.

SEA-SPIDERS (PYCNOGONIDA ; PANTOPODA), marine species related to the Arachnids, inhabit the shores or the depths of the seas, living on seaweed, hydroids and sponges. They are provided with 4 primitive ocelli perched in two pairs on an oculiferous tubercle on the cephalothorax ; as we have already noted, the retinæ are of a peculiar and characteristic inverted type [1] (Morgan, 1891 ; Korschelt and Heider, 1893 ; Sokolow, 1911 ; Schlottke, 1933) (Fig. 125).



Pycnogonid

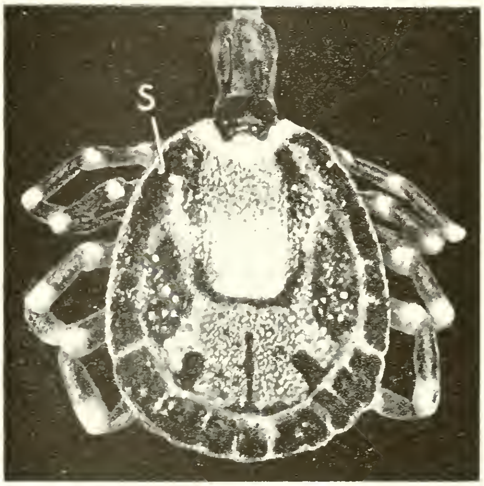


FIG. 222.—THE TICK, *AMBLYOMMA POMPOSUM*.

The two simple eyes, S, lie well posteriorly on the shoulder of the animal (specimen from Natural History Museum).

INSECTA

INSECTS form the largest class of Arthropods and their multitude of types is subdivided with reference to their possession of wings ; it is interesting that the complexity of their eyes varies directly with this characteristic, an association only natural in view of the demands made upon vision by a high degree of mobility.

(1) Sub-class APTERYGOTA (ἀ, privative ; πτέρυξ a wing), wingless forms, in which through a series of moults the adult differs little from the newly hatched insect except in size. They are the most primitive of insects, some species being marine, and when eyes are present they are simple in type.

THYSANURA—bristle-tails, of wide distribution in damp soil, some living between tide-marks or under stones or bark ; others (silver-fish) in bread-bins or books. Closely related are the eye-less DIPLURA.

PROTURA—minute creatures (2 mm.) living in moist soils under stones and bark, without wings, antennæ or eyes of any kind.

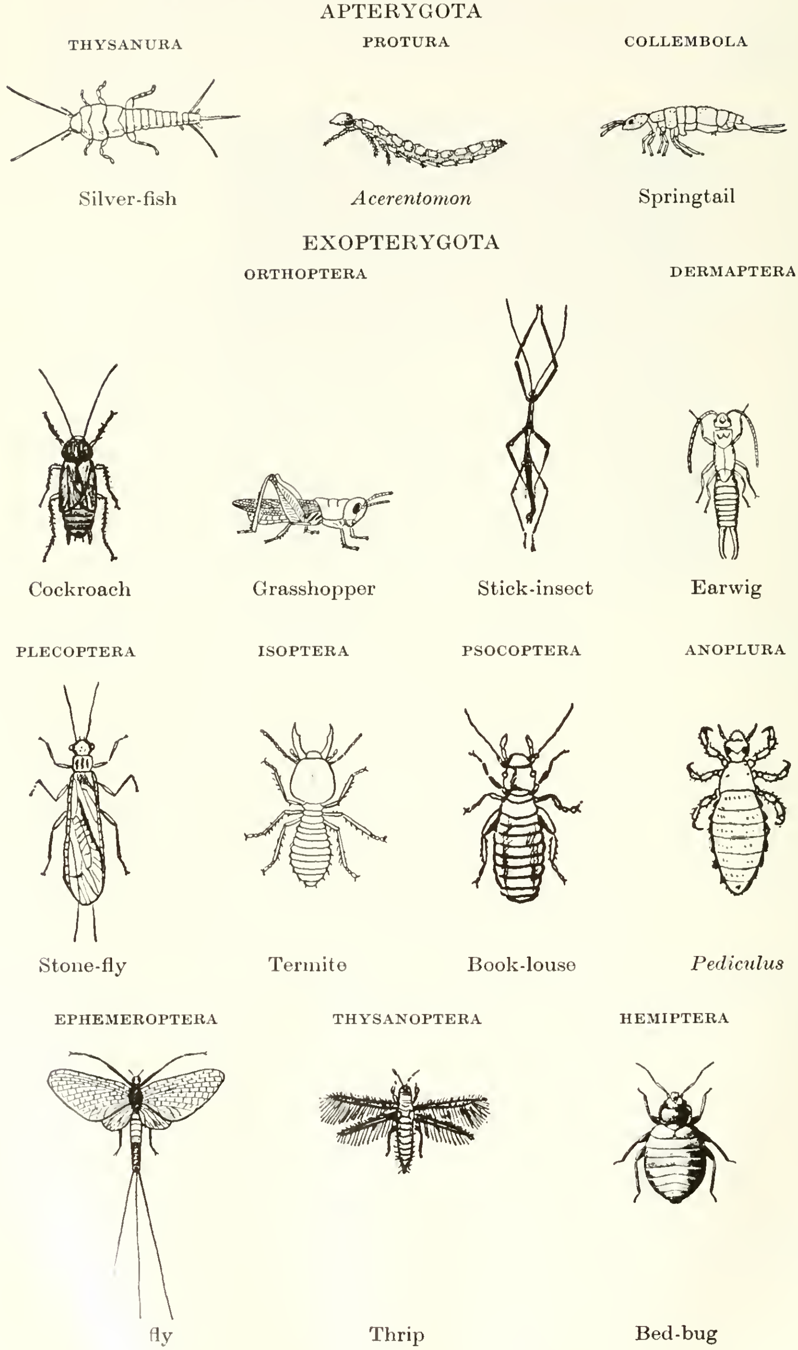
COLLEMBOLA—springtails, living under stones and leaves ; one species lives between tide-marks.

(2) Sub-class PTERYGOTA, provided with wings which, however, may be secondarily lost through highly evolved specialization. The sub-class is divided

[1] p. 150.

TYPICAL INSECTS : I

(*Drawn not to scale but approximately to a standard size.*)



TYPICAL INSECTS : II

(Drawn not to scale but approximately to a standard size.)

ENDOPTERYGOTA

NEUROPTERA

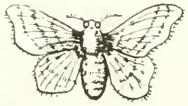
Lacewing

TRICHOPTERA

Caddis-fly

LEPIDOPTERA

Butterfly



Moth

COLEOPTERA

Colorado beetle, *Leptinotarsa*

Burying beetle, *Necrophorus*

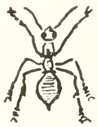
Rose-chafer, *Cetonia*

Fire-fly, *Photinus*

HYMENOPTERA

Bee, *Bombus*

Wasp, *Vespa*



Ant

DIPTERA

Blue-bottle, *Calliphora*

Gad-fly, *Tabanus*

Bee-fly, *Bombylius*

APHANIPTERA

Flea, *Pulex irritans*

into two, depending on whether their wings are developed externally (Exopterygota) or internally (Endopterygota) ; in the latter the wings become evident only in the adult (imago) stage.

(*a*) EXOPTERYGOTA, insects which undergo a series of moults marked by the gradual development of wings. The more important orders are :—

ORTHOPTERA—cockroaches, locusts, grasshoppers, crickets, stick-insects, praying mantis.

DERMAPTERA—earwigs.

PLECOPTERA—stone-flies, a small and little known order, the aquatic larvæ being found beneath the stones of mountain streams, and the slow-flying adults having a very short life.

ISOPTERA—termites living under ground without eyes.

EMBIOPTERA—a few species of insignificant tropical insects.

ZORAPTERA—a few species of minute insects resembling termites.

PSOCOPTERA—small plump, book-lice (winged or wingless).

ANOPLURA—biting or sucking lice, wingless, parasitic on man and animals and frequently disease-producing (*Pediculus*, *Phthirus*, etc.).

EPHEMEROPTERA—mayflies, the aquatic larvæ living up to 3 years, the delicate adult a few hours.

ODONATA—brilliantly coloured dragonflies and demoiselle flies with aquatic larvæ, the former unusually active, swift-flying and voracious, the latter more delicate.

THYSANOPTERA—the minute thrips, vegetarian in habit, living on flowers, leaves and decayed vegetation.

HEMIPTERA—bugs with a specially developed proboscis (rostrum) adapted for piercing and sucking, many of them beautiful and slender despite their name : land bugs including the bed-bug, water bugs varying from the giant fish-killer or the water-scorpion to the water boatman (*Notonecta*), the cicadas, the frog-hoppers, tree-hoppers, leaf-hoppers, the aphids (or green-flies) and the scale-insects.

(*b*) ENDOPTERYGOTA, winged insects which have a complete metamorphosis (egg, larva, pupa, adult) with a resting pupa (or chrysalis).

NEUROPTERA—lace-wings, alder-flies, scorpion-flies.

TRICHOPTERA—caddis-flies, with aquatic larvæ and moth-like adults with hair-covered bodies and wings.

LEPIDOPTERA—butterflies and moths.

COLEOPTERA—beetles, including over 200,000 known species, both terrestrial and water-beetles.

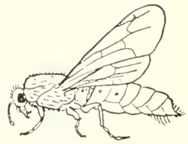
STREPSIPTERA—*Stylops*, minute insects, parasitic on other insects, particularly wasps and bees.

HYMENOPTERA—gall-flies, saw-flies, ichneumon-flies, bees, wasps, ants.

DIPTERA—two-winged flies, midges, gnats, mosquitoes and fruit-flies.

APHANIPTERA—the secondarily wingless fleas (jiggers, etc.), blood-sucking in habit and parasitic on birds and mammals.

In the larval form all insects possess simple lateral eyes (STEMMATA; στέμμα, a garland). The adult also frequently possesses simple eyes (DORSAL OCELLI), although they are absent or vestigial in many species, as in most beetles and mosquitoes, some families of flies, and noctuid moths; but in addition it is provided with MULTIFACETED COMPOUND EYES. To this generalization there are some exceptions in degenerative forms which are unprovided with compound eyes—the primitive wingless Collembola (Fig. 223), lice and parasitic fleas which possess only ocelli (Fig. 224), while species which live in darkness may be unprovided with eyes, such as the Protura, the driver ant of Africa, *Dorylus* (with the exception of the winged male), or most termites. The winged male *Stylops* has aggregate eyes composed of a multitude of ocelli so closely packed together as to resemble a compound eye, but the parasitic female which passes its whole life within its host, is unprovided with eyes.[1]



Male driver ant

FIGS. 223 AND 224.—INSECTS WITH OCELLI AND NO COMPOUND EYES (Natural History Museum, London).

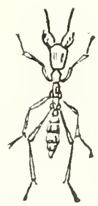
FIG. 223.—The springtail, *Archistoma besselsi* (Collembola).

There are 8 ocelli on each side and no compound eyes.

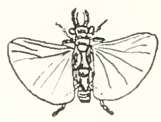
FIG. 224.—The bird-louse, *Trinoton aculeatum* (Anoplura).

There are 2 simple eyes (S) on each side and no compound eyes.

We shall see [2] that the compound eyes are the dominant organs in the adult insect, the simple eyes essentially accessory ; this is seen in the occasional disappearance of the latter as the former develop. Thus the larva of the water-beetle, *Dytiscus*, has 6 ocelli on each side of the head, but in the later stages of larval development the compound eye appears in front of them, first as a crescentic area on each side. At the stage of moulting the corneæ of the ocelli are shed with the cuticle and as the compound eye rapidly develops the bodies of the ocelli recede, remaining, however, permanently attached in vestigial form to the optic nerves.



Female driver ant



Stylops

[1] For the descriptive anatomy of the compound eyes of Insects, see p. 166 ; for that of the ocelli, see Hesse (1901), Merton (1905), Link (1908–9), Strohm (1910), Demoll and Scheuring (1912), Bugnion and Popoff (1914), Melin (1923), Homann (1924), Hamilton (1925), Zikan (1929), Wolsky (1930–31), Friederichs (1931), Verrier (1940), Lhoste (1941).

[2] p. 224.

FIGS. 225 TO 227.—THE COMPOUND EYES OF INSECTS.

FIG. 225.—The head of the dragon-fly, *Æschna californica* (Odonata) capped by two enormous crescent-like compound eyes (James Needham).

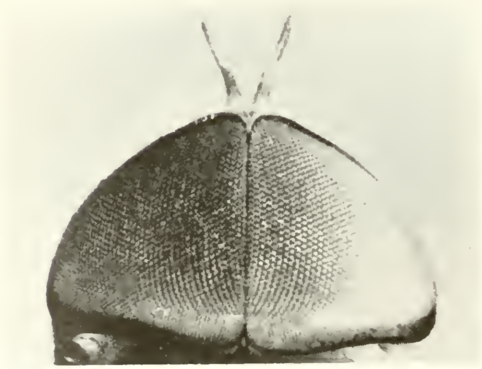


FIG. 226.—The male gadfly, *Ancala fasciata nilotica* (Diptera).

The immense compound eyes occupy the whole of the surface of the head (Natural History Museum, London).

FIG. 227.—The cave-bug, *Leotichius glaucopis* (Hemiptera).

From Malaya. Dorsal surface. The 2 prominent compound eyes (C) are largely spread over the ventral surface. There are 2 median ocelli (S) (Natural History Museum, London).

THE STEMMATA (OR LATERAL OCELLI) OF LARVAL OR PUPAL FORMS can in general be classified into two main types. The most elaborate organs are seen in the larvæ of Lepidoptera and Trichoptera; these are arranged in a group of variable size [1] on either side of the head, each separate individual of which takes the form of the single ommatidium of a compound eye with a cuticular corneal lens,

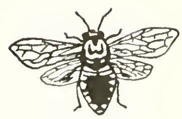
[1] E.g., 6 on either side of the head in the caterpillars of butterflies.

FIGS. 228 AND 229.—STALKED COMPOUND EYES.

FIG. 228.—A grouse locust, *Ophiotettix limosina* (Orthoptera).
The compound eyes (C) are placed on either side at the end of the stalk-like head. (One antenna is missing.) (Natural History Museum, London.)

FIG. 229.—The stalk-eyed fly, *Achias rothschildi* (Diptera).
The large compound eyes (C) are at the end of unusually long stalks (Natural History Museum, London).

a crystalline cone and a retinule of 7 sensory cells grouped around a rhabdome (Fig. 138) (Dethier, 1942–43). A more simple variety is seen in the larvæ of Tenthredinidæ (saw-flies) and Coleoptera. These usually have two lateral eyes of cupulate shape with a retina formed as a palisade of sensory cells under a lens-like thickening of the cuticle. The retinular cells are arranged in groups of two or three, each group around an elementary rhabdome which is not constructed for the reception of images. More rudimentary forms occur such as the



Sawfly

simple pair of visual cells with two overlying pigment cells which form the eye of the larva of the midge, *Ceratopogon*, or the few light-sensitive cells lying in a shaded pocket in the pharyngeal skeleton of the larva of the house-fly, *Musca* (Fig. 99) (Welsh, 1937 ; Debaisieux, 1939).

THE DORSAL OCELLI OF ADULTS were described and figured as early as 1678 by the French scientist, de la Hire (Figs. 149, 227, 230). They are usually three in number arranged in triangular form, one median and anterior and two lateral and posterior on the dorsal aspect of the

FIGS. 230 AND 231.—UNUSUAL COMPOUND EYES IN INSECTS (Natural History Museum, London).

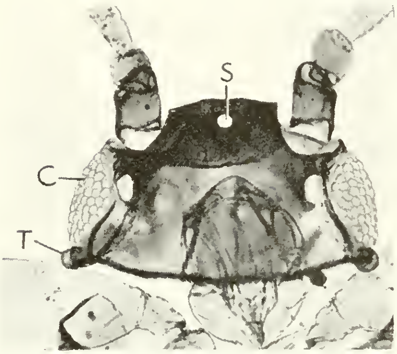


FIG. 230.—The aphid, *Dactynotus obscuras* (Homoptera).

There are 2 compound eyes (C) one on each side of the head, and, in winged forms, 3 ocelli on the vertex of the head, the median one of which is marked S. In the family Aphididæ there is in addition a prominence, the triommatidion (T), of unknown function, bearing 3 facets at the base of each compound eye. This organ is always present, even in those forms in which a compound eye is lacking.

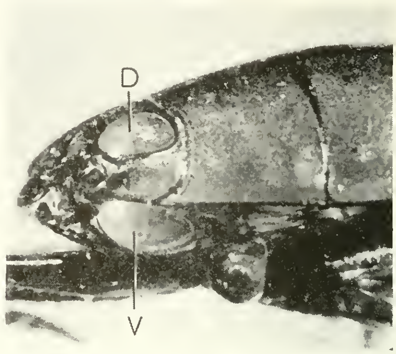


FIG. 231.—The Whirligig beetle, *Dineutus grossus* (Coleoptera).

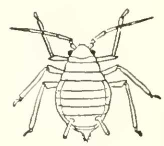
There are 2 compound eyes on each side of the head, one dorsal (D) for aerial vision, and one ventral (V) for vision under water.

head between the compound eyes ; but they are small and inconspicuous, being often hidden by scales as in moths or hairs as in bees. In some species of ants belonging to the sub-family Myrmicinæ, the anterior ocelli are double or binary in type (Weber, 1947). In others, such as Orthoptera, the ocelli are vestigial ; in general, their degree of development shows some correlation with that of the wings (Kalmus, 1945). As a rule they resemble in structure the more simple type of stemmata, being comprised merely of a group of visual cells associated with rhabdomes lying beneath a common cuticular lens (Fig. 108).

THE COMPOUND EYES OF ADULTS are laterally situated on the head and form the essential visual organ (Fig. 149). They are large and prominent and vary in complexity from the small organ of the worker of the ant, *Solenopsis*, which lives underground and is provided with 6 or 8 facets, to the elaborate organ of dragon-flies (Odonata) with up to 28,000[1] ommatidia (Imms, 1935) (Figs 225 to 227). Occasionally the compound eyes are enormous, literally occupying the whole surface of the head, as is seen in the gad-flies (Tabanidæ) (Fig. 226); usually they are situated on the surface of the head, sometimes they stand out prominently as in the praying mantis (Fig. 734), but occasionally they are perched on long stalks (Figs. 228 and 229). Exceptionally two compound eyes are differentiated in function, such as in the whirligig beetle, *Dineutus*, which has a dorsal compound eye for aerial vision and a ventral for vision under water (Fig. 231).[2] A unique organ is seen in the Aphid family ("green-fly") in which an additional trifaceted organ, the TRIOMMATIDION, is found at the base of each compound eye (Fig. 230); the function of this organ is unknown but it is present even in those forms of aphids which have no compound eyes.

Dragon-fly

Whirligig beetle



Aphid

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[1] p. 172.
[2] Compare the eye of *Anableps*, p. 324.

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