The most conspicuous sense organs are the eyes, antennules and antennae.

Compound Eyes

1. **Structure.** Prawn has one pair of black and hemispherical eyes. Each eye is mounted on a short, movable and two-jointed **stalk,** which is lodged in an **orbital notch** at the base of rostrum. Each eye is made of a large number of independent visual elements or units, called **ommatidia** (Gr., **ommation,** little eye). Such eyes are called the **compound eyes**. These are characteristic of Arthropoda and do not occur

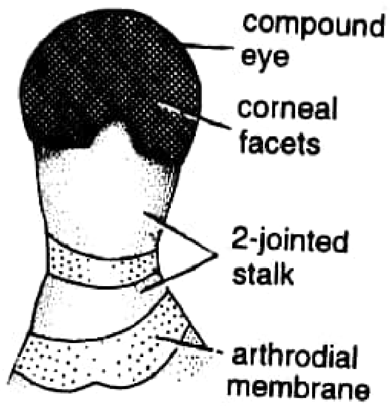

Fig. 29. *Palaemon.* Compound eye.

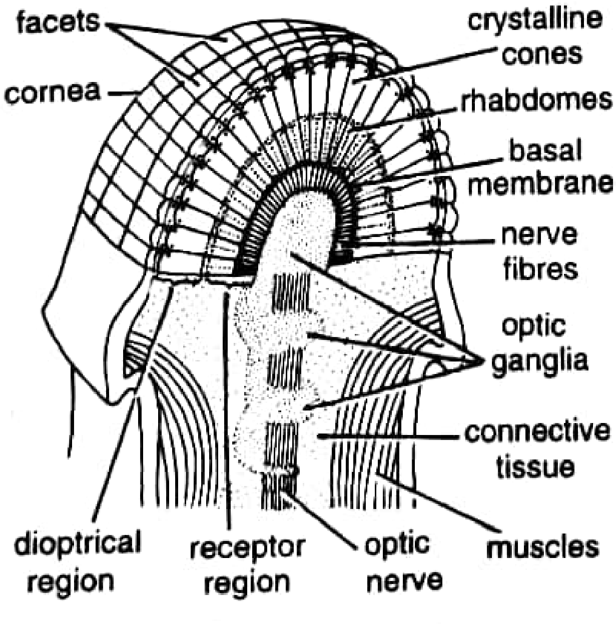

Fig. 30. *Palaemon.* L.s. of compound eye showing arrangement of ommatidia.

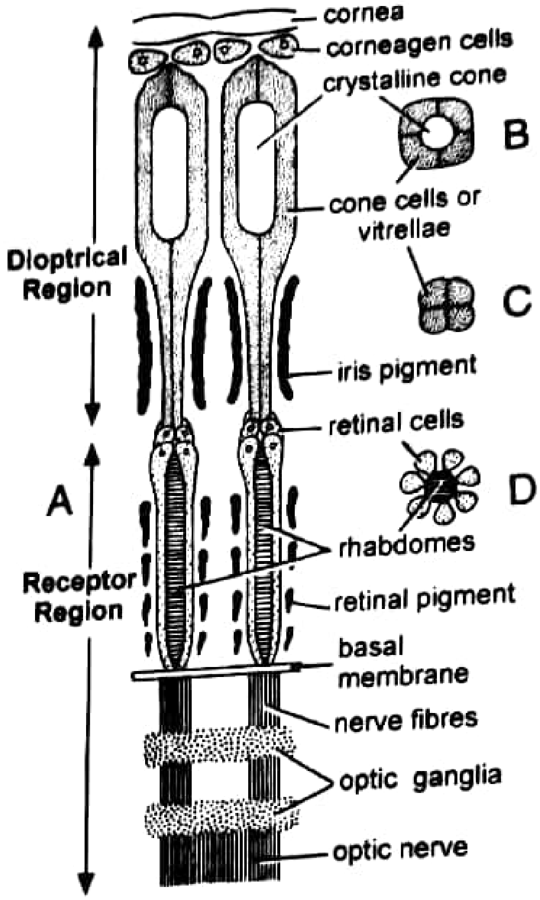

Fig. 31. *Palaemon.* Histological structure of compound eye. **A.** Two ommatidia in L.S. (semi-diagrammatic). **B.** T.S. of an ommatidium through cone cells. **C.** T.S. through basal ends of cone cells. **D.** T.S. through retinal cells.

elsewhere in the animal kingdom. All the ommatidia (about 2,500) are arranged radially and are similar in structure, each consisting of many cells arranged along its central axis. Their description is as follows :

(a) Cornea. The outermost convex layer of eye forming **cornea** is the transparent cuticle. In surface view, cornea exhibits a large number of squares or **facets** by clearly visible lines, thus giving the appearance of a graph paper. In insect eyes, the facets are not squares but hexagons. Below each facet lies one ommatidium.

(b) Corneagen cells. Each corneal facet thickens in the centre to form a **biconvex corneal lens**. Beneath the lens lie two **corneagen** cells which are modified epidermal cells and secrete a new cornea as soon as the old one is cast off in moulting.

(c) Cone cells. Beneath the corneagen cells lie four elongated **cone cells** or **vitrellae** which

constitute a transparent, homogeneous **crystalline cone**. Inner ends of cone cells are long and tapering.

The part of eye, from cornea up to extreme ends of cone cells, is known as the **dioptrical region,** which focusses light upon the inner sensitive part or **receptor region** of eye.

(d) Rhabdome and retinal cells. Inner ends of cone cells lie upon an elongated, spindle-shaped rod, the **rhabdome**. It has a transversely striated appearance. Rhabdome is secreted and surrounded by a group of seven elongated **retinal cells.** Rhabdome and retinal cells together form the **receptor region** of eye. Inner ends of retinal cells rest upon a **basal membrane** beyond which they are continuous with sensory nerve fibres of **optic ganglia** which are connected with brain by the **optic nerve**.

(e) Chromatophores. Each ommatidium is cut off from its neighbours by a sheath of movable, amoeboid, dark **pigment cells** or **chromatophores** which are arranged in two series. Outer series lying along the cone cells is called **iris pigment,** and inner series separating the rhabdomes is called **retinal pigment**. Amoeboid pigment cells take up different positions according to the variations in the intensity of light.

2. Mosaic vision. Working of compound eye is very complex. It is deficient in focussing ability and clarity of image. But, such an eye is efficient for picking up motion and for **peripheral vision**. It functions as a very efficient organ for photo-reception. Mounted on a movable stalk, it can move on the head in much the same manner as the antenna of radar, and gives the animal almost 360-degree vision. Each ommatidium is capable of producing a separate image of a small part of the object seen. Therefore, in prawns and other arthropods possessing compound eyes, the image of the object viewed consists of several dark and light tiny pieces or spots, so that the total image of an object formed is a sort of a flat **mosaic.** Moving objects can thus be detected. The vision effected is said to be **mosasic vision** because of its similarity to mosaic art work.

The nature of composite image formed varies according to different intensities of light. Thus two types of images are formed. This is made possible by the movement of pigment cells.

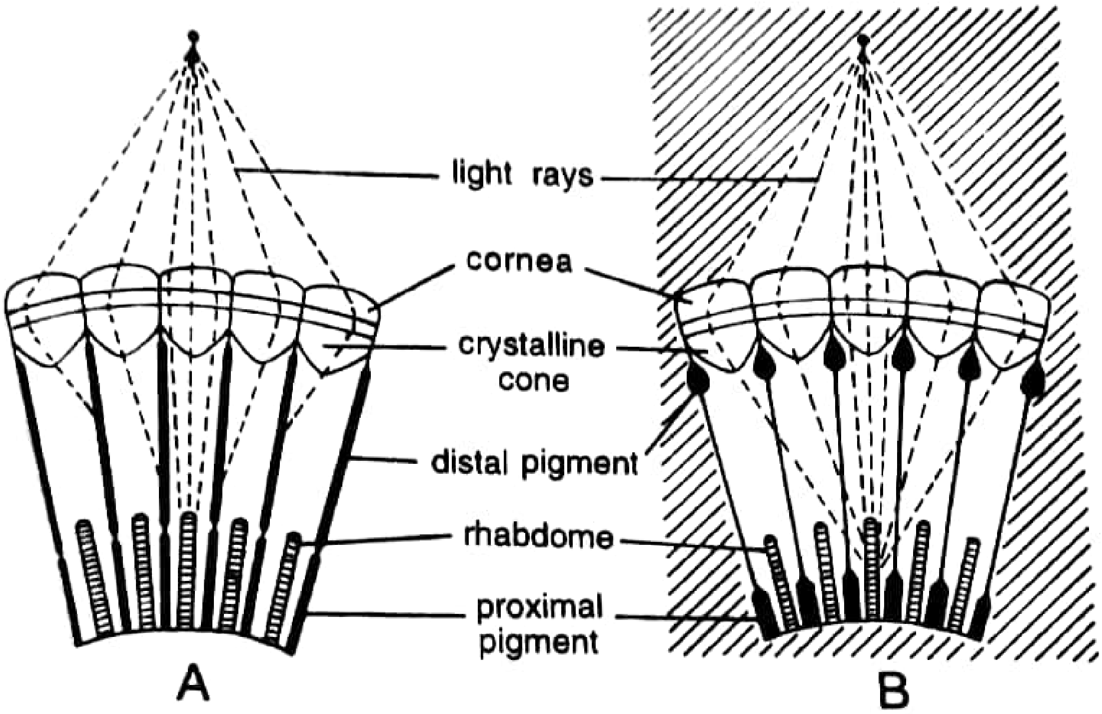

Fig. 32. *Palaemon.* Diagrammatic representation of image formation by a compound eye. **A.** Apposition image in bright light (day vision). **B.** Superposition image in dim light (night vision).

pposition image. In bright light (during (b) Superposition image. In dim light *(a)* ***Apposition image.*** In **bright light** (during daytime), the pigment cells spread in such a way that they completely isolate optically the adjacent ommatidia. No light can pass through from one visual unit to the other. In this condition the rays of light, which strike the cornea obliquely, are absorbed by the pigment cells without producing a visual effect. Only those rays of light which fall perpendicularly upon the cornea, can travel through the ommatidium and reach the rhabdome to form a point of image. As a result, the complete image formed is a mosaic of several components placed in juxtaposition in which the slightest movement is readily detected. In other words, each ommatidium responds to a fragment of the total field of vision and then these fragmentary images are fitted together into a single general picture. It is known as a mosaic or **apposition image**. Its sharpness depends upon the number of ommatidia involved and the degree of their isolation from one another. In butterflies, which are night-blind, the eyes are permanently set in this condition and are suited to see only in bright light. The image formed by this type of eye is never very good. It functions best at short distances only. Thus, most arthropods are always short-sighted.

(b) Superposition image. In **dim light** (during night), the pigment cells migrate and become separated into distal and proximal pigments, so that the neighbouring ommatidia no longer remain optically isolated but work in unison. In this condition even oblique rays of light are capable of forming a point of image after passing through a number of ommatidia in their way. As a result, an overlapping of the adjacent points of image occurs so that a continuous or **superposition image** is obtained. It is not sharp but the animal gets some sort of idea of the objects moving about in the surrounding. In some insects, like moths and fireflies, the eyes are permanently set like this, so that they are well adapted to see at night but are day-blind.

The prawns, like most arthropods, seem to adjust their eyes to form both types of images according to the prevailing intensity of light.

The **optic nerve** carries impulses (electro-chemical waves of energy) to the brain, where they are interpreted and registered as an upright **mental** image.

[II] Statocysts

1. Structure of statocyst. Statocysts are a pair of small, white, bead-like cuticular and hollow

(Soumalainen, 1962; White, ...

19.3.3 Alternation of generations (Cyclical Parthenogenesis)

A number of insects combine the advantages of parthenogenesis with the advantages of bisexual reproduction by an alternation of generations. This occurs, for instance, in the Cynipidae, which are commonly bivoltine, a generation of parthenogenetic females alternating with a bisexual generation. *Neuroterus lenticularis* (Hymenoptera) forms galls on the underside of oak leaves in which the species overwinters. Females emerge in the spring and lay eggs. The eggs of some females undergo meiosis but, since in the absence of males they cannot be fertilised, they remain haploid and so give rise to males; other females produce eggs in which no reduction division occurs and which give rise only to females. In this way the bisexual generation arises, the insects emerging from catkin galls in early summer. After mating, the females of this generation lay eggs which are fertilised and which produce the females of the following spring generation.

Aphids have a more complex alternation of generations with several parthenogenetic generations occurring during the summer (Fig. 284). Sometimes, as in *Aphis fabae*, an alternation of host plants also occurs. The first generation emerges on spindle in spring from overwintering eggs. It consists entirely of females, the fundatrices, which may or may not produce wingless generations of fundatrigeniae before a winged generation, the migrantes, appears. These migrate to a bean plant and produce wingless alienicolae, of which there may be many successive generations, but ultimately these produce the sexuparae, some of which are winged and return to the spindle while others are wingless. The former produce females, the latter winged males which then join the females; they mate and winter eggs are produced. All these generations except for the last reproduce parthenogenetically and consist entirely of females. In some species, such as *Tetraneura*, only one class of sexuparae is produced and these individuals give birth to both male and female sexual forms, an instance of amphitoky.

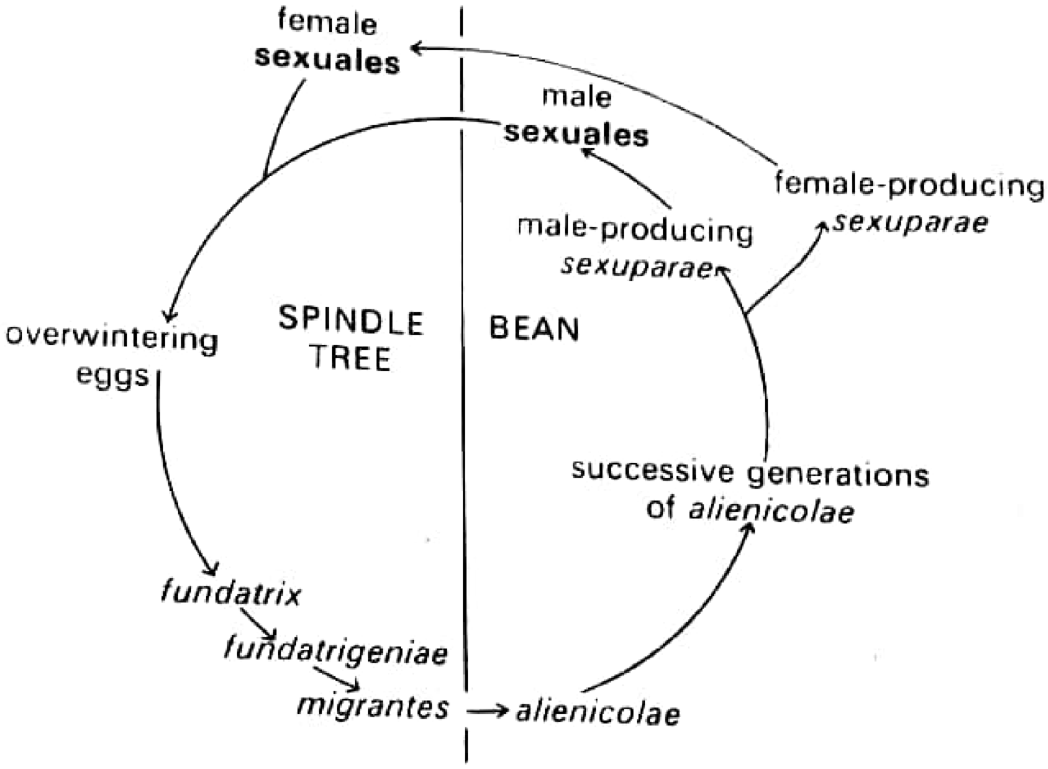

Fig. 284 Alternation of sexual and parthenogenetic generations in *Aphis*. Sexual generation in bold type; wholly female parthogenetic generations in italics (from Imms, 1957)

Female aphids are produced apomictically (but see Lees, 1966), while males result from the loss of an X-chromosome to a polar body at meiosis, although no reduction of the autosomes occurs. Thus an egg acquires the XO constitution of the male. The production of males is ultimately under environmental control, but how the environment controls chromosome behaviour is not known (Lees, 1966).

Spermatogenesis in male aphids is characteristic, ensuring that all the eggs produced are female. At the first meiotic division two kinds of spermatocytes are produced: some with an X-chromosome and some without. The latter degenerate and so only the former undergo the second meiotic division and only one type of sperm, containing an X-chromosome, is produced. Hence the fertilised eggs can only be female.

The aphids reproduce very rapidly, combining the advantages of parthenogenesis with viviparity and paedogenesis, so that successive generations are extensively telescoped. In the tropics, where conditions are continuously favourable, parthenogenesis may continue indefinitely without the intervention of a sexual generation.

An alternation of generations may also occur in Cecidomyidae (see below).

19.4 Paedogenesis

Sometimes immature insects mature precociously and are able to reproduce, this phenomenon being known as paedogenesis. It arises from an unusual hormonal balance (p. 835) and most insects reproducing paedogenetically are also parthenogenetic and viviparous. Development of the offspring which are produced paedogenetically usually begins in the larval insect, but these insects may be grouped according to the stage which gives birth to the offspring.

In *Miastor* and *Micromalthus* the larvae give birth to other larvae or, occasionally, lay eggs. Paedogenesis occurs in *Miastor* only under very good or poor nutritional conditions. Young larvae are set free in the body cavity of the paedogenetic larva and they feed on the maternal tissues, eventually escaping through the body wall of the parent. Under average nutritional conditions normal adults are produced.

Micromalthus has five reproductive forms: adult males, adult females, male-producing larvae, female-producing larvae, and larvae producing males and females. The species has a complex heteromorphosis (Fig. 285). The form emerging from the egg is a triungulin and this moults to an apodous larva which can develop in one of three ways. It can develop through a pupa to a normal adult female, or it can moult to a larval form which gives rise paedogenetically to a male, or to a paedogenetic larva which produces triungulins. Male-producing larvae lay a single egg containing a young embryo, but the egg adheres to the parent and when the larva hatches it eats the parent larva. If, for some reason the parent larva is not eaten, it subsequently produces a small brood of female larvae (Pringle, 1938; Scott, 1941).

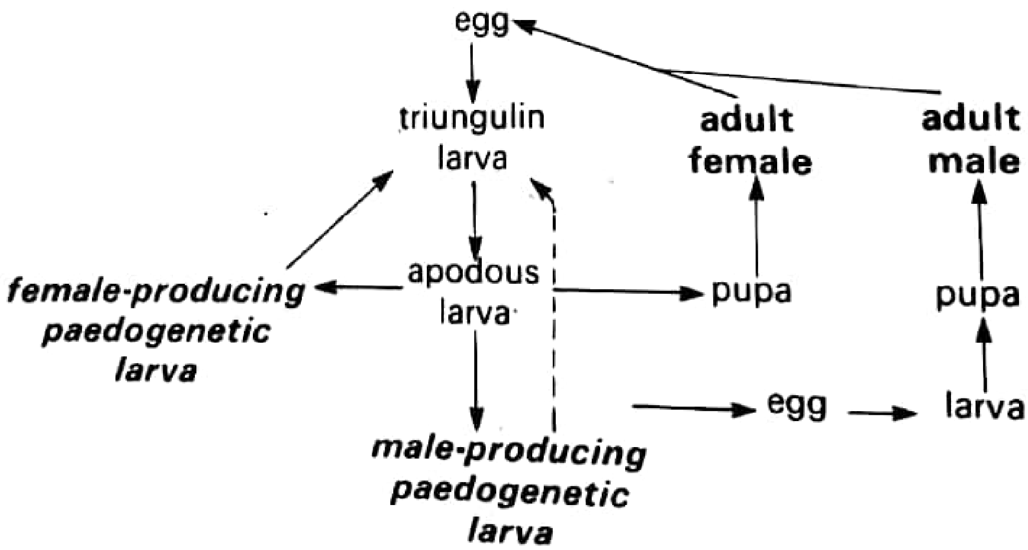

Fig. 285 Diagram of the life history of *Micromalthus*. Reproductive forms in bold type; paedogenetically reproducing larvae italicised (based on Pringle, 1938)

In the cecidomyids *Tekomyia* and *Henria* pupal forms give birth to larvae. The larvae of these insects are of two types: one type produces a pupa and, ultimately, a normal adult; the other forms a hemipupa, a rounded structure with, in *Henria*, vestiges of wings and legs. A brood of larvae, commonly between 30 and 60 of them, escapes from the hemipupa by rupturing the cuticle (Wyatt, 1961). Wyatt (1963) also suggests that pupal paedogenesis occurs in *Heteropeza* (*Oligarces*). Larvae are released into the haemocoel of the parent larva, but they escape from a form which he interprets as a hemipupa in which they can survive, if the conditions are moist, for up to 18 months. Paedogenesis is the normal method of reproduction in these insects and although normal adults may be produced it is not certain that they are capable of producing viable offspring.

Paedogenesis also occurs in aphids. Although the young are not born until the aphid has reached the adult stage, their development may begin before she is born while she is still in the ducts of the grandparental generation. Development of the offspring continues through the larval life of the parent.

The bug *Hesperoctenes* is an example of a paedogenetic form in which fertilisation occurs. Some last instar larvae are found with sperm in the haemocoel as a result of haemocoelic insemination (p. 371). These sperm fertilise the eggs which develop in the ovaries of the larva.