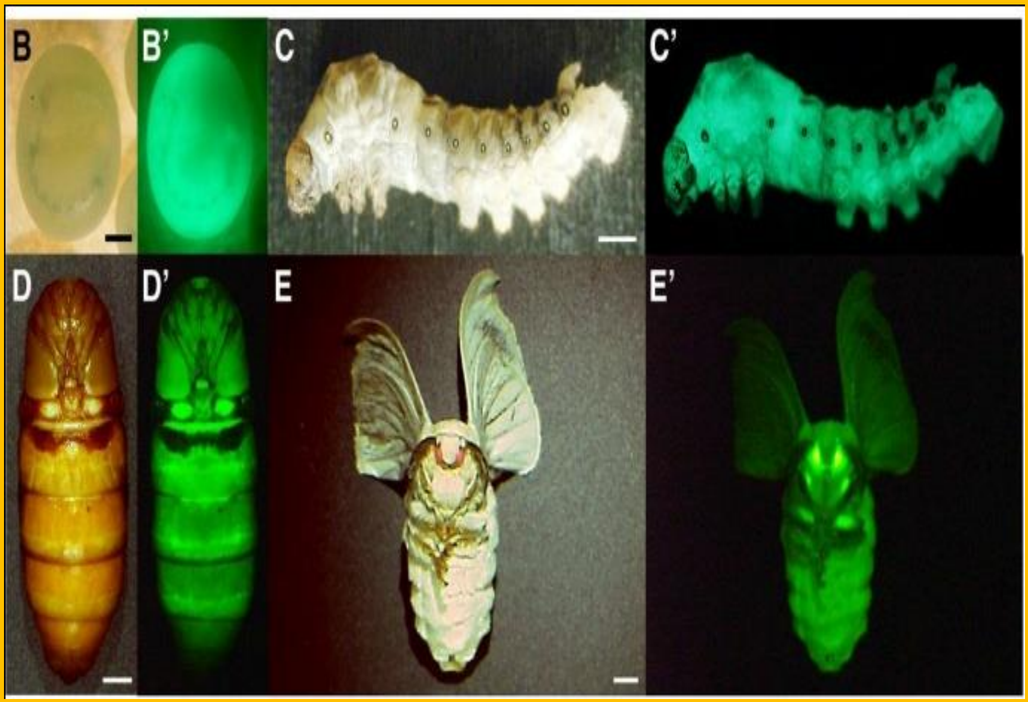
MSCZO-611

Entomology (Morphology, Physiology & Development Biology)

M. Sc. IV Semester



DEPARTMENT OF ZOOLOGY

SCHOOL OF SCIENCES

UTTARAKHAND OPEN UNIVERSITY

Entomology (Morphology, Physiology & Development Biology)

(MSCZO-611)

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UNIT 1: HEAD

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1.2 Introduction
1.3 Structure of the typical eye
1.3.1 Modification of eye
1.3.2 Structure of Ommatidium
1.3.3 Mechanism of image formation
1.3.3.1 Diurnal insects
1.3.3.2 Nocturnal insects
1.4 Structure and modification of antennae
1.5 Mouth parts of typical insects
1.6 Modifications of mouth parts in different insects
1.7 Summary
1.8 Terminal Questions and Answers

1.1 OBJECTIVES

The unit describes the characteristics of the phylum Arthropoda and the all classes contained in this phylum.It is a piece of detail information on the class Insecta and twenty-nine orders. At the end of this unit, you should be able to differentiate between the major Arthropoda classes and all the orders of class Insecta. This unit gives an account of various segments of the body of the insects. It introduces the reader to various appendages found on the head and thorax of the insect.

1.2 INTRODUCTION

Arthropoda is the largest phylum of the animal kingdom.It includes about 1,13,40,000 species in all habitats.This constitutes about 83%of all the known animal species on the earth.In Insecta and other arthropods,the body is segmented and each segment has a dorsal sclerite (the tergum),joined to a ventral sclerite (the sternum) by the lateral membranous areas,the pleura.In insects, the segments are grouped into the head,thorax and abdomen, in which the various basic parts of the segments are greatly modified or lost. The head is the center for feeding and sensation where feeding organs and sensory organs are present.It consists of six fused segments, which are ocellary, antennal, intercalary,mandibular,maxillary and labial.

TYPES OF GRASSHOPPER HEAD PARTS

The body of an insect is divided into three parts (regions) Head, Thorax, and Abdomen.

Head: It is the main part of the body, which formed by six segments and attached to the thorax. These segments are ocellary antennal, intercalary, mandibular, maxillary and labial. The head generally assumes the following three definite positions with the body axis. **(i) Hypognathus.** In this position the long axis of the head is vertical and the mouth parts are ventral. The median line of the head forms right angle with the median line of the body,*e.g.*grasshopper of orderOrthoptera. **(ii) Prognathus.** Here the long axis is horizontal and mouthparts are anterior in position, so the median line of the head is parallel to the median line of the body,*e.g*. beetles of order Coleoptera. **(iii) Opisthognathus.** In this type, the head is directed backward and the mouthparts are posteroventral,*e.g*. Bugs of order Hemiptera.

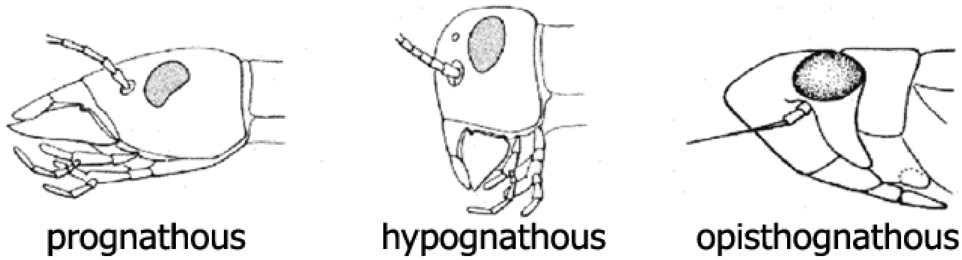


Fig .1.1: Three types of Insect Head

Head Sutures Part of an Insect:

1. Frons: This area on the anterior face lies between or below the epicranial arm just below the vertex, which extends from the frontal suture to the clypeus and up to the base of both mandibles and median ocellus, is situated on sclerite. **2. Clypeus.** This is a lip-like area between the fronto-clypeal suture and the labrum. **3. Vertex.** The parts of the head above the frontal suture are the vertex, which lies above the frons. The ocelli and antennae are situated in this region. **4. Epicranial** suture. It is an inverted Y - shaped suture that lies posteriorlybetween the eyes, whose stem begins on the back of the head and crosses the vertex and fork on the face. **5. Genae.** These are the lateral walls of the Head situated below and behind the eyes. **6. Compound eyes.** It is paired structure situated in the dorso-lateral position to the head capsule. Each eye is surrounded by a narrow ring-like ocular sclerite. **7. Ocelli.** These are located in between the compound eyes and are generally three in number. **8. Antennae**. These are situated in the antennal socket between the compound eyes. **9. Tentorium.** The endoskeleton of the head is known as the tentorium. Thus, tentorium is composed of four principal parts namely, the anterior arms, posterior arms, corporatentorium or central mass, and dorsal arms.

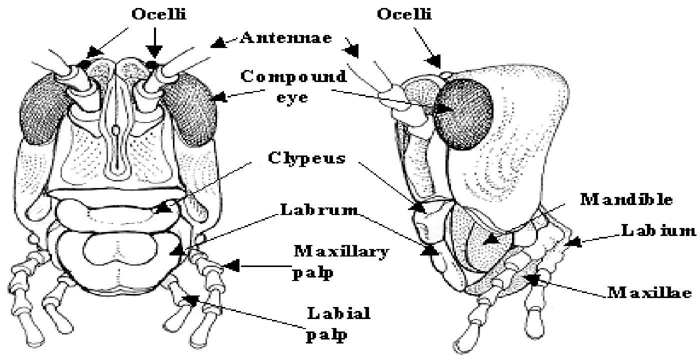


Fig 1.2: Head Sutures Part of Insects.

1.3 STRUCTURE OF TYPICAL EYE

A compound eye is a visual organ found in arthropods, such as insects and crustaceans. It may consist of thousands of ommatidia, which are tiny independent photoreception units that consist of a cornea, lens, and photoreceptor cells which distinguish brightness and colour.

1.3.1 MODIFICATION OF EYE

The compound eye is **made up of many "ommatidia", the basic units that the insect eye is comprised of**. Each one is kind of like an eyeball in the fact that it has a lens that focuses light and has pigments (opsins) for detecting color

SENSE ORGANS OF INSECTS (WITH SPECIAL REFERENCE TO LOCUSTS:

Receptor whereby the energy of a stimulus arising outside or within the insect is transformed into a nervous impulse refers to sense organs. The sense organs of insects include both the excerptors' (they perceive the stimuli arising in the external environment) and interceptors (excited by stimuli arising within the body) along with the proprioceptors.Based on functions performed by the sense organs they are classified into following main groups:

1. Photoreceptor organs
2. Chordotonal organs

3. Olfactory organs
4. Gustatory organs
5. Tactile organs
6. Humidity and temperature receptors.

1. Photoreceptors. The most primitive photoreceptive organs of insects are represented by the paired small papillae on the apex of the head of the mucoid maggots. In the current age insects following photo receptors are worthy to note.

(*a*) Ocellus. These refer (ocelli) to the simple eyes of insects. In insects, two types of ocelli are found. **(*i*) Dorsal Ocelli.** They are found in the nymphs of hemimetabolous insects and almost all adult insects. Typically, they are three in number and situated in a triangle. They are shifted to the vertex in Diptera and Hymenoptera. In locusts,the median ocellus is located on the frons, while the paired ocelli areon the vertex. A typical insect ocellus bears the following main parts: **(*i*) the cornea.** Is a transparent cuticular structure that is arched or raised to form the outer investment of the ocellus? **(*ii*) The corneagen layer.** This layer secretes and supports the lens and is composed of colourless transparent cells.

(*iii*) Retina. It's composed of visual cells which are sensory neurons. An ocellus consists of a group of photoreceptor cells or retinules each ending in nerve fibre which leads to the brain. The outer end of each photoreceptor cell forms a rhabdome cuticle covering the group of photoreceptor cells, and forms a thick, biconvex transparent lens.

(*iv*) The Pigment cells. Between the retinulae ocelli contain accessory cells bearing pigments, which have been noticed in a few cases.

Functions: The ocelli are simple light-sensitive organs activating the central nervous system and thus play a key role in maintaining the diurnal rhythm. They are well adapted for the quick perception of light, changing in its intensity. They are, however, mostly incapable of forming images because of the wide angular separation of their rhabdoms and the images are focused far behind the retina.

(*ii*) The stemata or lateral eyes. As the name, it indicates that these eyes are lateral in position. They differ from dorsal ocelli as they are innervated from the optic lobes of the brain. They vary in number from a single pair to six pairs amongst holometabolons immature forms. Adult insects generally have a single pair of lateral eyes on the head.

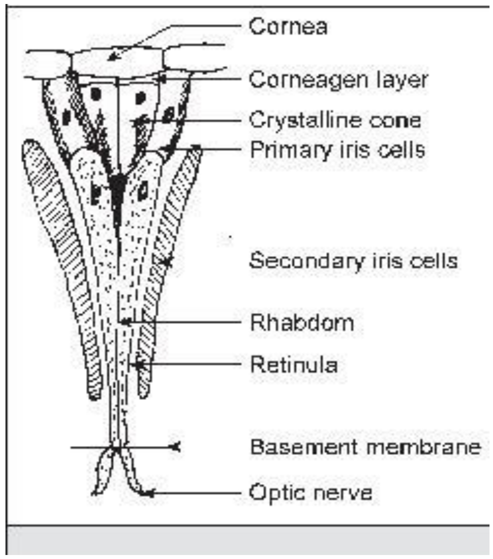


Fig 1. 3: Longitudinal Section of an Ocellus.

Functions: They are capable of differentiating the shapes and colours of the objects and can form images on the rhabdoms.

(***b***) **Compound eyes.** The compound eyes of insects are composed of a large number of structural units called ommatidia. The compound eyes are the chief visual source or organs of Machilidae and the majority of the pterygotes. The cornea of compound eyes is divided into a large number of facets often equal to that of ommatidia. It should be noted that the size of the facets is mostly proportional to the square root of the height of the eye.

1.3.2 STRUCTURE OF OMMATIDIUM

Each ommatidium consists of a cornea, which in land insects is curved and acts as a lens. Beneath the cornea is a transparent crystalline cone through which rays converge to an image at the tip of a receptive structure, known as the rhabdom**.** The basic difference between the ocellus and the compound eye is that:

(*i*) The ocellus bears a dome-shaped common lens for all visual cells while in the compound eye each visual cell is provided with an independent lens.

(*ii*) Lens is cuticular.

(*iii*) Pigment cells are lacking.

(*iv*) Retina is made up of only four retinula cells. (*v*) Axons form ocellar nerve.

(*vi*) Ocellar nerve terminates into the par intercerebralis. (*vii*) Cone is absent.

(*viii*) Ocelli do not form the image of an object.

Fundamentally each ommatidium consists of a dioptric or optical apparatus receiving the light and a sensory or retina forming the image. In addition to its various components of ommatidium include.

(*i*) Cornea. It's the outermost part of the ommatidium. It is a transparent, colourless and biconvex-modified cuticular area often termed as a facet or lens. It is shed during each moult.

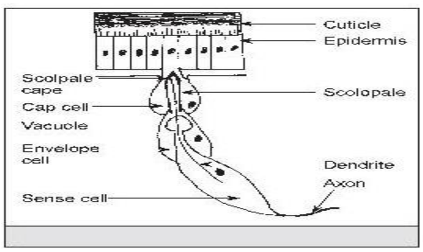
(*ii*) Corneagen layer. They are the epidermal or hypodermal cells lying behind the cornea. A group of two corneagen cells secrete a single lens.

(*iii*) Cone cells. Just Beneath the corneagen layer of the cornea, there are four distinct cells that secrete a transparent body known as a crystalline cone or semper cells.

(*iv*) Retinula cells. The crystalline cone is followed by a long retina forming the basal part of an ommatidium. It is formed from a group of similar seven pigmented visual cells. The visual cells secrete an internal optic rod or rhabdom. The portion of rhabdom formed by each cell is termed as rhabdom. These rhabdomeres of all seven retinula cells extend the whole length of the Retina. In addition to these cells, there are deeply pigmented cells which surround the cells of thecrystalline cone and the corneagen layer, referred to as primary iris cells. Elongated pigment cells which surround the primary iris cells and the retinula are termed as secondary iris cells.

2. Chordotonal organs. These are also called auditory organs which are usually compound structures made up of a spindle-shaped group of scolopophores. They are intravisceral mechanoreceptors. Both ends of these organs are attached to the integument of the insect. Each scolopophore consists of (*i*) a cap provided with a terminal ligament apically and acts as a scolopale cap, (*ii*) the scolopale is formed within an envelope cells that contains sensory cuticle rod, (*iii*) the sensory cells as the third cells of the scolophore which extends dendrite process apically. It runs through the vacuole, scolopale and finally terminates at the end knob of the scolopale. These organs are generally found in the abdominal appendages and wing bases of insects. It is reported that besides sound receptors they are also used for various purposes including proprioception and the reception of internal pressure changes and mechanical vibrations. The highly specialised chorodontonal organs are:

(*i*) **Johnston's organ.**Except for Collembola and Diplura, all other insects possess the Johnston organ in the second antennal segment. This organ was first seen and reported by Christopher Johnston and consists of a variable number of radially arranged sensilla. These are attached at one end to the second and third intersegmental membrane and at the other end to the wall of the second segment. The axons of the sense cells of these organs run back and enter the antennal nerve. The antennae also contain a large number of campaniform and chordotonal sensilla. The Johnston organs respond to the movements of the antennal flagellum and thus act as not merely the photoreceptors but also perceive air currents during flight, vibrations through substratum during walking, and through water surface at swimming



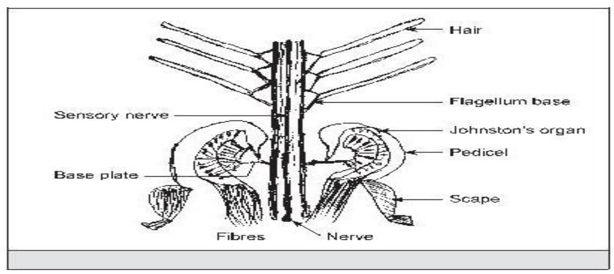


Fig 1.4: Chordotonal Organ: Basic Structure. Johnston's organ of male mosquito.

(***ii***) **Tympanal organs functions.** These are paired structures made up of a thin cuticular membrane known as the tympanum. They are associated with tracheal air sacs and chordotonal sensilla. These tympanal organs have been reported occurring at the base of each fore tibia in the members of Tettigonoidea and Grylloidea. In grasshoppers, the tympanal organ is situated on each side of the first abdominal tergum and externally surrounded by a cuticular ring. Internally, there is a sensory organ known as Mullers organ, which is formed by a group of numerous scolopophores and connected to the metathorax ganglion by the auditory nerve

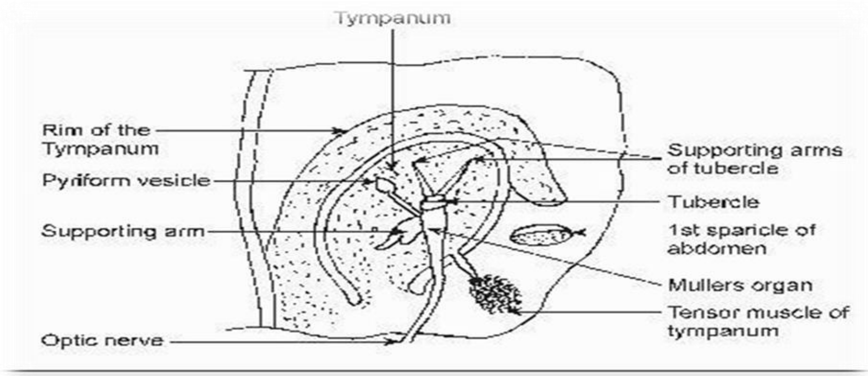


Fig 1.5: Tympanal organs functions.

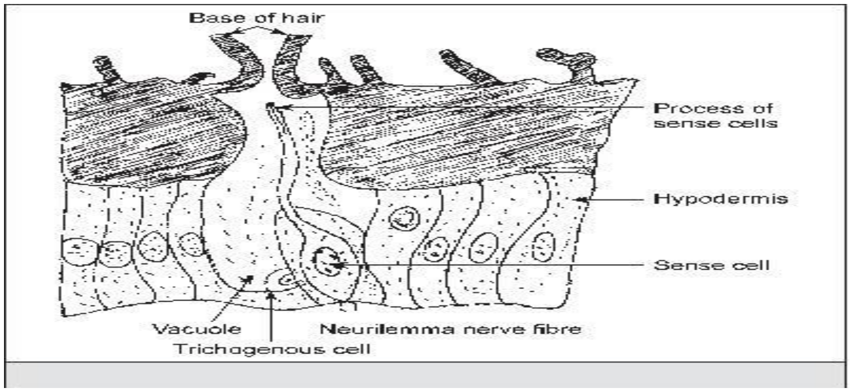
(*iii*) Olfactory organs. These sense organs provide a sense of smell that is mediated by chemical stimuli in a gaseous state at low concentration. There are, however some receptors that appear to mediate responses to chemicals in both gaseous and aqueous phases in some aquatic beetles. Antennae are supplied with the organs of smell – *Locust*.

(*iv*) Gustatory organs. These provide a sense of taste that is mediated by chemical stimuli acting with liquids at high concentrations. In the terrestrial insects, the gustatory chemoreceptors are mostly confined to the mouthparts, wall of true oral or pharyngeal cavity rarely on the tarsi and distal end of tibia as found in the butterfly, moths, honey bees,*etc*.

(*v*) Tactile organs. Tactile hairs sensitive to touch are located on various body parts, particularly, the antennae, palps and distal leg segments. They are simple articulated sensory hairs and are commonly called sensilla. They are made up of a cuticle and articulated within the socket with the body wall. The trichoid sensillum is formed by two cells, the hair by the trichogen cell and the socket by the tormogen cell. Both of these cells are epidermal.

The tactile hairs of the antennae and lower segments of the legs perceive earth-born vibrations in terrestrial insects and water surface vibrations in aquatic insects.

(***vi***) **The Humidity and temperature receptors**. These are the most important organs,especially meant for controlling the desiccations in insects. Humidity receptors have been identified by pendiculus in the form of a peculiar tuft like cuticular sensilla and in many species as basiconic, trichoid and placoid sensilla. With the help of these sensilla, ants predict the rains well in advance that is why they migrate to safer places along their eggs, larvae and pupae prior to the onset of monsoon



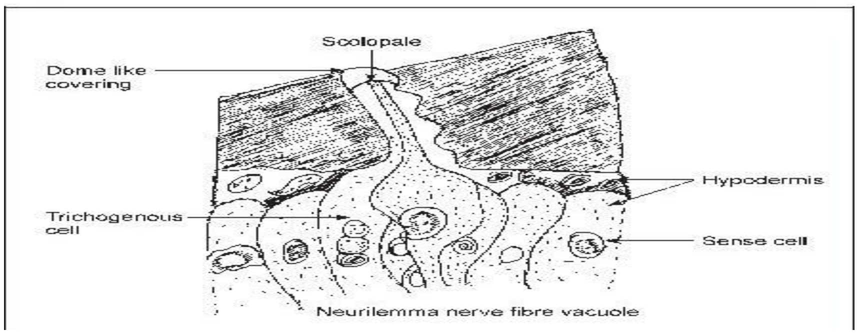


*Fig 1.6: The Tactile insect Hairs of Cereus. Campaniform Sensillum from the Cereus (*Campaniform sensilla *are a class of mechanoreceptors found in insects, which respond to local stress and strain within the animal's cuticle.)*

1.3.2 MECHANISM OF IMAGE FORMATION

Each ommatidium consists of a cornea, which in land insects is curved and acts as a lens. Beneath the cornea is a transparent crystalline cone through which **rays converge to an image at the tip of a receptive structure, known as the rhabdom**.

Image Formation:

Compound eyes form image with the help of inputs received from ommatidia. Each ommatidium forms a separate image of a small part of the object. Thus, the image formed consists of several pieces and is crude. This type of vision is called mosaic vision. Compound eyes of arthropods can form two kinds of image depending on the intensity of light:

Apposition image

Superposition image

Apposition Image: The compound eyes form apposition image in the bright light. In bright light, both proximal and distal pigments extend and act as a screen to prevent light rays from passing from one ommatidium to another. The light rays remain restricted to the axial region of the crystalline cone and rhabdomes. As a result, only those rays which fall perpendicularly on the cornea and pass through rhabdome form the point of an image. The rays which fall obliquely on the cornea are absorbed by the pigment and do not produce any visual effect. Thus, each ommatidium responds to a patch of light from the visual field and overlaps little with the neighboring ommatidia forming a point of an image. The final image is formed by combining all these points formed by the stimulated ommatidia. This is, therefore, mosaic vision as it results from small pieces put together.

Apposition eyes are the most common form of eye, and are presumably the ancestral form of the compound eye. They are found in all arthropod groups.

Superposition Image: The superposition image is formed in the dim light. In the weak light, both proximal and distal pigments retract. The ommatidia do not remain optically isolated and the light rays can pass from one ommatidium to another. As a result, the oblique rays as well as those which fall perpendicularly on the cornea and pass through rhabdomefrom the point of an image. Thus, each ommatidium responds to the light rays which had entered through different corneal facets. The final image is continuously formed by overlapping of the adjacent points of images.

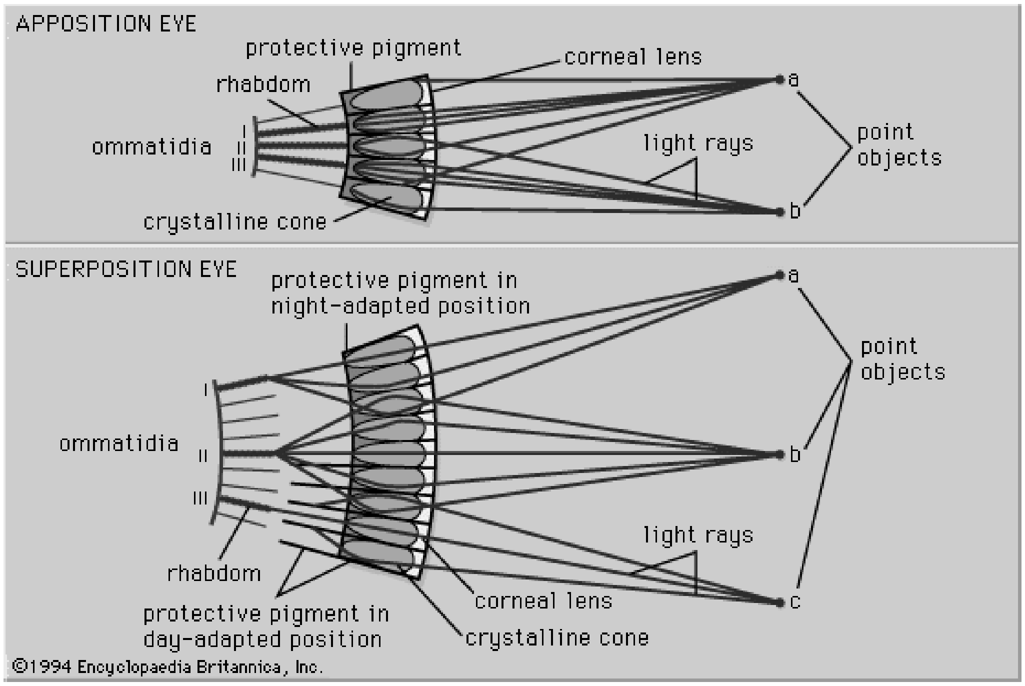


Fig 1.7:Image formation in apposition and superposition eyes.

1.3.3.1 DIURNAL INSECTS

This word describes a creature that is most active during the day. Many of the species we see daily fall into this category. Robins, eagles and sparrows are diurnal. Insects, such as, bees pollinate the flowers that bloom in daylight. And of course, no matter how late a person might like to stay up, humans are a diurnal species.

1.3.3.2 NOCTURNAL INSECTS

This is a word used to describe an organism that is most active at night. Nocturnal animals include mammals, such as bats, cats, opossums, rats and mice. And then there are the owls that hunt down those rats and mice. Many kinds of insects are also nocturnal. They play an important role in pollinating plants that open their flowers at night.

1.4 STRUCTURE AND MODIFICATION OF ANTENNAE

The Head Appendage includes the antennae and mouthparts.

Antennae. These are multi-segmented and may be divided into three parts. **1. Scape.** This is a basal segment of antenna and attached with head.**2.Pedicle.** It is the second segment of antenna, which is shorter than scape and it bears sensory apparatus known as Johnston organs. **3. Flagellum.** This part is also known as clavola.

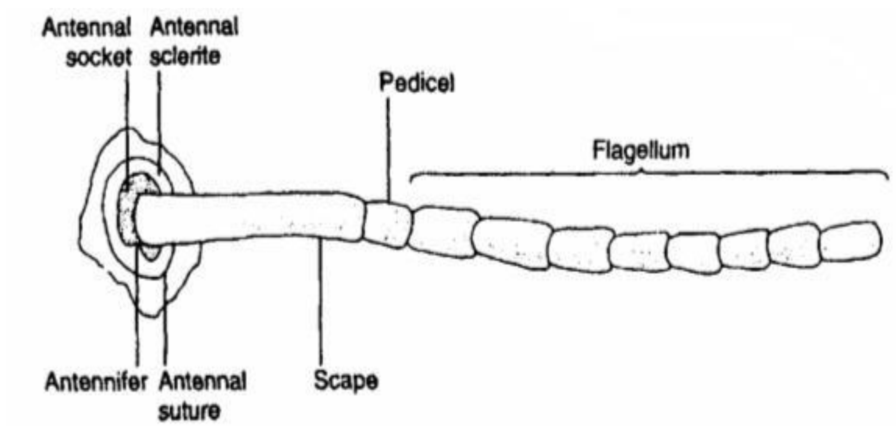


Fig 1.8: Typical type of antennae.

The function of antennae. The main function of antennae is sensory, which is modified according to the use and need of the insect the antennae are found in different types in the male and female,*e.g.* mosquito. The hearing organs often known as Johnston's organs situated in the second segment of antenna, e.g. male mosquito, green butterfly and yellow wasp,*etc*. The sound producing organs are attached to the antennae of some insects belonging to the order Coleoptera and Orthoptera, e.g. beetles and crickets.

The butterflies are having some transmuting and receiving organs with their antennae. Insects of different orders have various types of antennae.

Filiform — This is a thread-like antenna,where all the segments are nearly uniform in thickness and have no prominent constriction at the joints, such as in orders Orthoptera, Coleoptera and Lepidoptera namely grasshopper and ground beetle.

Setaceous— This type of antenna is tapering, e.g. dragonfly.

Moniliform — All the segments of this antenna are globular in shape and of uniform thickness looking like a string of beads, e.g. Isoptera that includes termites.

Pectinate— This is a comb-like antenna, which is found in sawfly.

Clavate— The distal segments gradually increase in diameter e.g., butterflies.

Capitate— The distal segments suddenly increase in diameter e.g., Khapra beetle.

Geniculate — In this type of antenna, the first segment is long, the second is short and flagellum is made of small segments which are bent on the scape just like a bent knee in the order Hymenoptera, e.g. Honey bees.

Fusiform–the basal and distal segment of this antenna are smaller and thin while middle segments are larger just like a radish. The last segment is modified into hook like structure order Lepidoptera–insect mouth,*etc*.

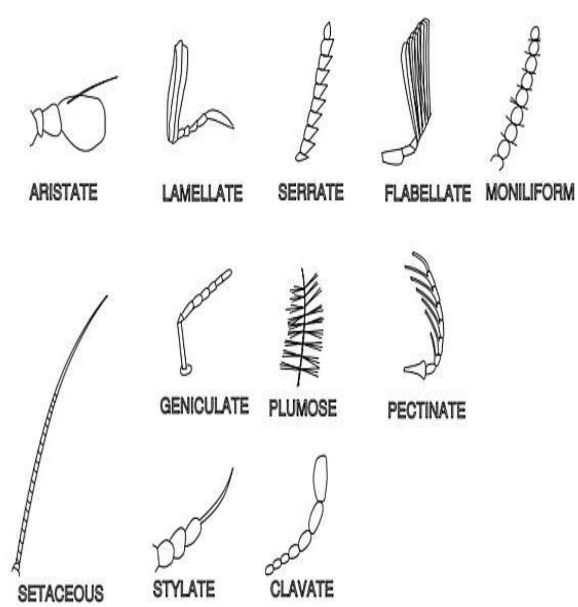


Fig. 1. 9: Different types of Insect Antenna.

1.5. MOUTH PARTS OF TYPICAL INSECT AND MODIFICATIONS OF MOUTH PARTS IN DIFFERENT INSECTS

Mouth Parts of Insects

The insect mouth parts are considered to be the diverse forms. Fundamentally, they (mouth parts) include hypopharynx, one pair of mandibles, one part of maxillae, posterior lower lip-labium. The mandible, maxillae and labium represent modification of typical paired appendage of three pairs of body segment. The typical anterior part of insect mouth is labrum. The mouth parts of insects can be divided into different groups depending upon the type of the food and feeding. The types of insect mouth part are mentioned below:

1. **Biting & Chewing Type or Mandibulate Type**. This type of mouth parts is found in cockroaches, grasshoppers, locusts, termites, wasps, booklice, bird lice, earwigs, dragonflies and other large number of insects.
2. **Piercing & Sucking Type.**
3. **Siphoning Type.**
4. **Chewing & Lapping Type.**
5. **Haustellate Or Sponging Type.**

1. Biting and Chewing Mouth Parts of Insect. These are types of mouth parts found in the insects belonging to order Orthoptera, Isoptera and Coleoptera, etc. The insects having such type of mouth part make hole on the leaves, seed, and fruit and cut irregularly. The biting and chewing type of mouth part consists of labium, epipharynx, mandibles, maxillae, labrum and hypopharynx. The labrum is flab like structure attached to the clypeus upper lips. It functions as protective upper lips and inner lips of mouth cavity, to protect mandibles and to grind the food into the mouth of insect.

The Epipharynx.This is an important structure with the upper surface of labrum. The epipharynx part bears taste buds in mouth of insects.

Mandibles. A pair of mandibles are located directly behind the labrum. Each mandible segmented, thick strong, triangular in structure upper surface flat. The mandibles are movable in mouth. There are two protractor muscles, viz. abductor and adductor muscles. The mandibles are primarily meant for chewing and grinding of the food.

The Maxillae. The maxillae are used for holding the food so that mandibles may perform their functions easily. Maxillae are a paired structure lying behind the mandibles. Maxillae are divided in different part as discussed below:

(i) Cardo. It is a triangular basal part attached to the head capsule and regulates movement of maxillae.

(ii) Stipes. It is a rectangular structure in maxillae situated above the cardo. There is a distinct sclerite known as palpifer to which the palpus is attached. **(iii) Galea**. They are outer lobe soft and segmented. The basal segment is termed as a parastipes. **(iv) Lacinia.** It is an inner lobe of maxillae. The inner side hard spine or teeth mallize in maxillae surface. (v**) Maxillary Palps.** It is an antenna like appendage attached with the lateral side of the stipes. The maxillary palp is attached as palpifer. Maxillary palp is a five segmented and sensory in function.

Labium. It is a lower lip of insect mouth cavity the labium appears to be a single organ, but consists of two parts, which have fused to form a functional structure. It is divided in different parts as (i) *submentum*, the flat leaf like basal part of the labium. (ii) *Mentum*, central part of the labium which bears a pair of three segmented pulp on its either side. (iii) *Prementum*, an upper portion of labium, which has four terminal lobes. The median pair is glossa and lateral paraglossa. These lobes are attached to lacinia and galea of the maxillae and are commonly known as ligula.

Hypopharynx. It is a tongue like structure in the mouth cavity. The salivary gland is believed to open in the mouth cavity of insects *via* hypopharynx.

2. **Piercing and sucking type mouth parts of insec**t. These types of mouth parts are found in mosquitoes and bugs. These are highly specialized mouth parts which are adapted for piercing and sucking blood and sap from animals and plants epidermis, respectively. Bug type is an exemplary type of mouth part found in the order Heteroptera and Family Pentatomidae, which are used for sucking sap from the plants. It contains a slightly different type of mouthparts,

whereall six parts, *viz*. paired mandibles, maxillae, labrum, epipharynx and hypopharynx are modified into needle like style and broad tubular like labium. The labrum-epipharynx, formed by the fusion of labrum and epipharynx, is the dorsal-most stylet covering the opening of the groove of proboscis. Hypopharynx is somewhat flat and double-edged sword stylet covers the food channel and has a salivary duct inside. Needle like mandibles lie on each side of the labium, epipharynx, the distal and being used for sucking sap/blood from human skin and other animal's skin. The maxillae are also needle like, distally serrated and located laterally hypopharynx in the groove of the proboscis. When the piercing is over, the dilator muscles contract and upward suction is created through the food channel by capillary action as a result of that the sap is sucked up from the plant cells by the turgor pressure into sucking chamber.

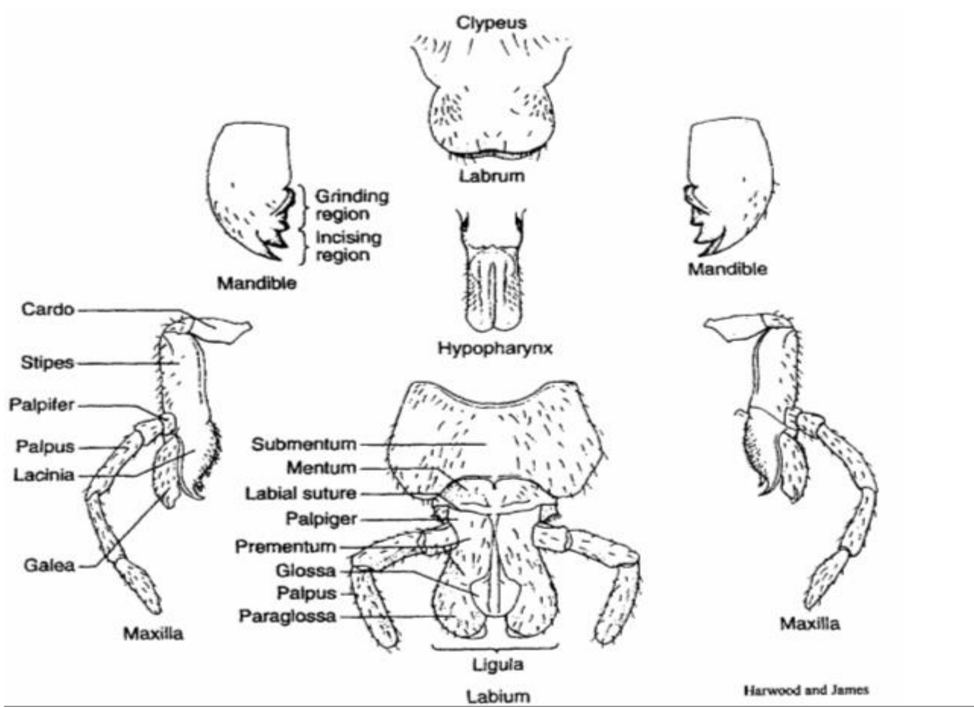


Fig: 1.10: Chewing and Biting type Mouth Parts of Insects.

3. Sponging Type Mouth Part: The sponging type mouth parts are commonly found in the order Diptera. It is found in non-blood sucking insects. The example is housefly. These mouth parts are highly modified and primarily used for feeding of liquid food soluble in saliva.It has a long labrum tapering and flap which originates from the distal margin of the rostrum and covers the anterior surface of the haustellum. The mouth is situated medially at the base of the labrum and hypopharynx. Mandibles are absent. Maxillae palp is single segmented and labium is fully developed and modified into long proboscis. It has three parts. (A) **Rostrum**. They are two small-lateral sclerites, which support a pair of single segmented maxillary palp of insect. (B) **Haustellum** is cylindrical shape and demarcated by a distinct long medio dorsal labial groove which work as the food channel. (C) **Labellum**is a distal portion of the labium and is also known as oral disc.

4. Chewing and lapping mouth parts. This type of mouthparts is found in the order Hymenoptera of class Insecta, e.g., ants, honey bees and wasps. These are generally used for collecting the pollen and nectar from the flowers. The mouth parts under labrum and mandibles are just like chewing type of mouth parts. Mandibles on the lateral side of labrum spoon shaped mainly adapted for molding the wax and for comb formation. Maxillae are either side of the labrum. The maxillae and labrum form flat and elongated structure and long blade like stipes, which the glossa form an extensible channeled organ with a small labellum at the tip. This proboscis is used to suck the nectaries of flowers.

5. Siphoning type mouth parts. The siphoning type mouth is found in the order Lepidoptera, which includes butterflies and moths. The proboscis is coiled type in moths, and is mainly used for sucking nectar from flowers. The labrum is not fully developed and a narrow transverse band is found at the lower edge of the clypeal region of the face labrum. The labrum on its lateral sides has small hairy lobes. The mandibles are usually reduced or absent. Its labium is undeveloped and this is represented only by segmented labial palp and a very small basal plate.

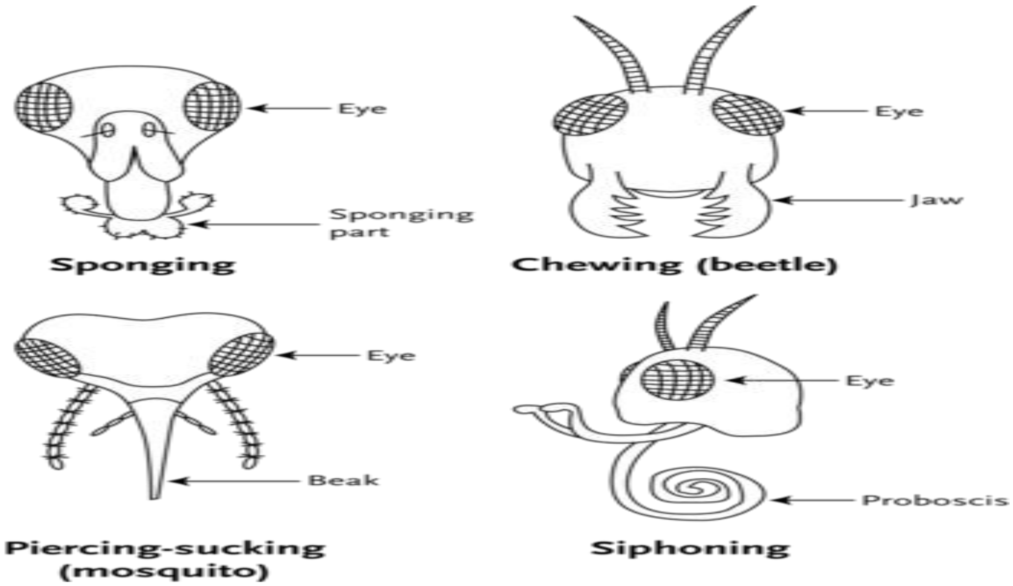


Fig 1.11: Various mouthparts in insects.

1.7 SUMMARY

The head of an insect is **composed of a series of segments, which are specialized for food gathering and manipulation, sensory perception, and neural integration**. The head bears the eyes (compound eyes and ocelli), antennae, and mouthparts. The anterior part of the head is the frons.Head harbours feeding and sensory organs and hence is the center for feeding and sensation.Head has six sutures and eight sclerites.

1.8 TERMINAL QUESTIONS AND ANSWERS: MCQ

1. **Which of the following statements is true about Entomology?**

   (a) The study of Birds

   (b) The study of Insects

   (c) The study of Microbes

   (d) The study of parasitic worms

Sol: (b) The study of Insects.

2. **Which of the following are the main characteristic features of an Insect?**

    (a) Pair of antennae

    (b) Three pairs of legs

    (c) Pair of wings

    (d) All of the above

    Sol: (b) Three pairs of legs.

3. **Insects, which feed on one type of food, are called _______.**

    (a) Polyphagous

    (b) Monophagous

    (c) Entomophagy

    (d) None of the above

    Sol: (b) Monophagous.

4. **Insects are classified into the phylum_______.**

    (a) Nematoda

    (b) Mollusca

    (c) Arthropoda

    (d) Platyhelminthes

    Sol: (c) Arthropoda.

5. **Which of the following statements is true for Entomophagy?**

    (a) Refers to eating birds

    (b) Refers to eating insects

    (c) Refers to eating fishes

    (d) None of the above

    Sol: (b) Refers to eating insects.

6. **The total number of abdominal legs in the larval stage of the mustard sawfly is ______.**

(a) 2 pairs

(b) 4 pairs

(c) 6 pairs

(d) 8 pairs

Sol: (d) 8 pairs.

7. **Which of the following structures is not the part of the insect head capsule?**

(a) Vertex

(b) Antennae

(c) Pronotum

(d) Tentorium

Sol: (c) Pronotum.

8. **What is the middle part of an insect body present between the head and the abdomen called?**

(a) Thorax

(b) Head

(c) Abdomen

(d) None of the above

Sol: (a) Thorax.

Long question:

1. Describe the various types of mouth parts found in insects
2. Describe the sutures found on the head capsule of an insect
3. Explain the different type and typical type of insect antenna.

REFERENCE

- P.K.Sehgal, (2017).Fundamental of Agricultural Entomology, first edition, Kalyani publishers New Delhi. Pp1-399.

UNIT 2: THORAX

2.1 Objectives

2.2 Introduction

2.3 Structure of typical Leg

2.3.1 Modification of different Legs

2.4 Structure of a typical Wing

2.4.1 Types of Wings

2.4.2 Hypothetical Wing Venation

2.4.3 Wing Coupling Mechanisms

2.4.4 Flight Mechanism

2.5 Summary

2.6 Terminal Questions and Answers

2.1 OBJECTIVES

The unit describes the characteristics of the phylum Arthropoda and the all classes contained in the phylum.It gives a detail information on the class Insecta and 29 order. At the end of this unit you should be able to differentiate the major Arthropoda classes and all order of this class Insecta. This unit gives an account of various segments of the body of the insects. It introduces the reader to various appendages found on the head and thorax of the insect. By the end of this unit you will be able to describe the various modification of legs and wings of the insects.

2.2 INTRODUCTION

Arthropoda is a largest phylum of animal kingdom.It includes about 1,13,40,000 species in all habitats.This constitutes about 83%of all the known animal species on the earth.In Insecta and other arthropods,the body is segmented and each segment basically has a dorsal sclerite (the tergum),joined to a ventral sclerite (the sternum) by the lateral membranous areas,the pleura .In the insects the segments are grouped into the head,thorax and abdomen, in which the various basic parts of the segments are greatly modified or lost.In the previous chapter, the detailed description of head is given. Head is the center for feeding and sensation where feeding organs and sensory organs are present. This type of grouping of segments into body regions is called tagmosis and each region is called tagmata.Thorax is the center for locomotion.The Legs and wings are present on this region, it consists of three segments.

2.3 STRUCTURE OF TYPICAL LEG

Insect legs are typically **6-segmented (coxa, trochanter, femur, tibia, tarsus, pretarsus) usually having only one trochanter and lacking a patella**. The tarsus is subdivided and there is typically a 2- clawed pretarsus.

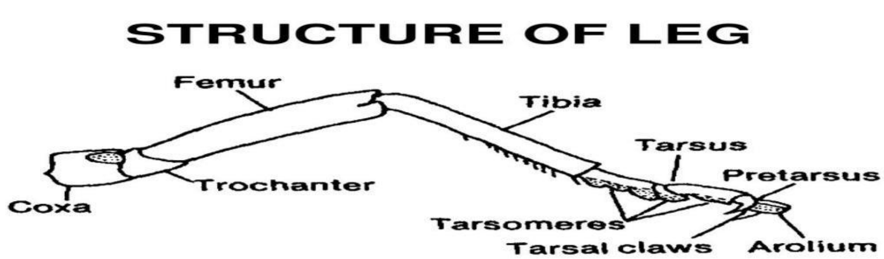


Fig 2.1 Structure of typical Leg of Insects.

2.3.1 MODIFICATION OF DIFFERENT LEGS

Thoracic region appendages.

There are two types of appendages: (A) Legs (B) Wings

A. Legs. The insect usually has three pair of legs which are located on the ventral side of thoracic region they are modified for different purposes and are categorized as running type, clinging type, jumping type. A typical leg consists of the following parts.

(**a) Coxa is basal segment and attaches the leg with thorax.** The coxa fits the cup like structure of the body. Coxa is generally freely movable. (b) The Trochanter is small second parts of the leg which articulate with coxa and fixed with femur. (c) Femur is a largest and powerful part of the insect leg. (d) Tibia is slender like structure, usually long and provided with downward projecting spines into which helps in climbing. (e) Tarsus is fifth segment of the insect leg. It is divided into two or five segments. (f) Pretarsus is the last terminal segment of the leg which is represented by complex set of claws which bear one or more pads. The have undergone many modifications and have been adapted to a wide variety of functions, including swimming, prey capture, pollen collection and digging.

(a) Cursorial Legs of Insect. These are almost similar to that of walking legs and are adapted in such a way to avoid slipping, e.g. ants, earwigs.

(b) Ambulatorial Legs of Insect. It is the generalized from of an insect legs, which are usually adapted for walking, e.g. Bugs.

(c) Clinging Legs of Insect. The clinging legs are smaller and flat. The clinging legs are found in lice etc. The Tarsi is single segmented and each segment ends in a powerful claw which works against a tibial process, e.g. louse.

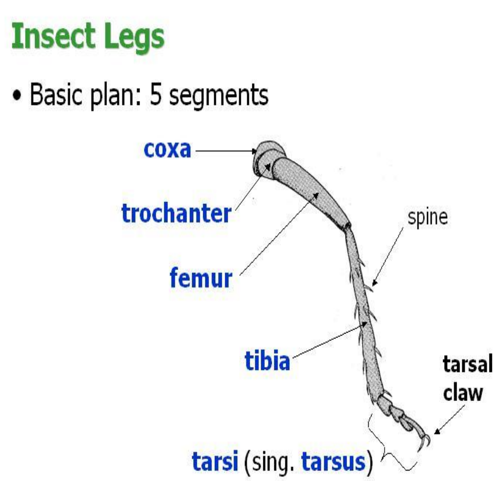
(**d) Pollen Collecting Legs of Insect**. The hind legs of the honeybees are adapted for carrying pollen from the flowers. The coxa, trochanter and femur are normal inshape, while the tibia of hind legs is dilated and covered with long dense hair thus forming a pollen basket which is primarily for storing the pollen grains parts of flowers. The first tarsi segment is flat and its inner surface is densely closed with several rows of short stiff spines forming a brush known as scopa. It helps the bees in collecting the pollen adhering to the hair of its body.

(e) Jumping Legs of Insect. This type of legs is developed in grasshoppers and beetles, where the femur of the hind leg gets enlarged and accommodates the powerful tibial muscles. These muscles help in jumping the insect, e.g. trochanter muscles.

(f) Sound Producing Legs of Insect. These sounds are made in two genendciolyer trances legs typically adapted for producing sound where the femur of hind leg of male insect like grasshopper or cricket is provided with the row of file on its inner side. These femoral file work against the outer surface of each tergum or costal margin of the forewing thereby producing a sound. Many beetles produce sound, usually by rubbing one pars of the (a scraper) against another part of the file.

(g) Natatorial Legs of Insect. The legs of several aquatic insects are modified in such a way that they facilitate swimming, e.g. water beetle. The coxa and trochanter are simple and smaller whereas the tarsus is five segmented and last terminal segment is triangular and pointed.

(h) Suctorial and Sucking Type Legs of Insect. The Tibia is comparatively smaller and flat.Tarsus is five segmented, and first and third segment modified into a swollen ball like structure and provided with stiff spines at their margins. They are also helpful in sticking with grass and leaves. These legs are also developed for sexual purpose in which the coxa and trochanter of the first legs are small.



2.2 Typical type leg of insect.

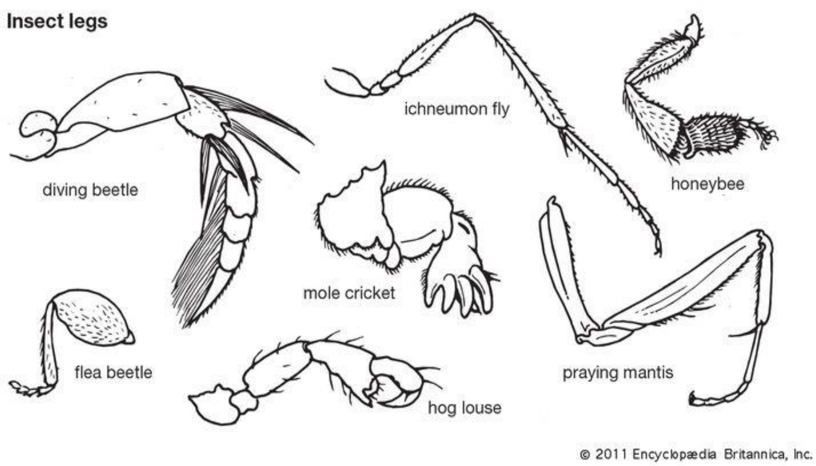


Fig 2.3. Different type of insect legs.

2.3 STRUCTURE OF A TYPICAL WING

Wings of the Insect

Generally, two pairs of wings are present, which are the outgrowths of the bodywall along the lateral margin of thorax. The presence of wings is one of the most characteristic features of the insects and provides one of the most useful Taxonomic aid to identify the insects. The wings are of course the organs of aerial locomotion in most cases, but like the legs they have undergone extensive adaptive modification in Insects. In the order Diptera, there is only one pair of wings and the hind wingsare modified into halteres.

Elytra. In the insects of order Coleoptera, the forewings get much hardened to form horny sheath, which protect the outer membrane and inner membrane of hind wings of insect. Hemelytra: this is well started in hemipteran insects, where the forewings are thickened at their basis like elytra and reaming as soft membranous at distal parts. That is why they are frequently termed as hemelytra. Halteres–the hind wings of order Diptera (housefly) are modified into knobbed Thread like balancing organs known as halteres. Haltere is a balance organ of House-fly.

Wing structure.The wing appears as a thin or transparent darkly fan like flattened membranous structure. The basal sclerites help in articulation of wing with the thorax as they rotate with one another. The wing bears a specific pattern of venation which is derived from unique arrangement of veins. The veins provide mechanical support and folding to the wings. They play important role in determination of direction of the wind, wing movement and navigation during flight.

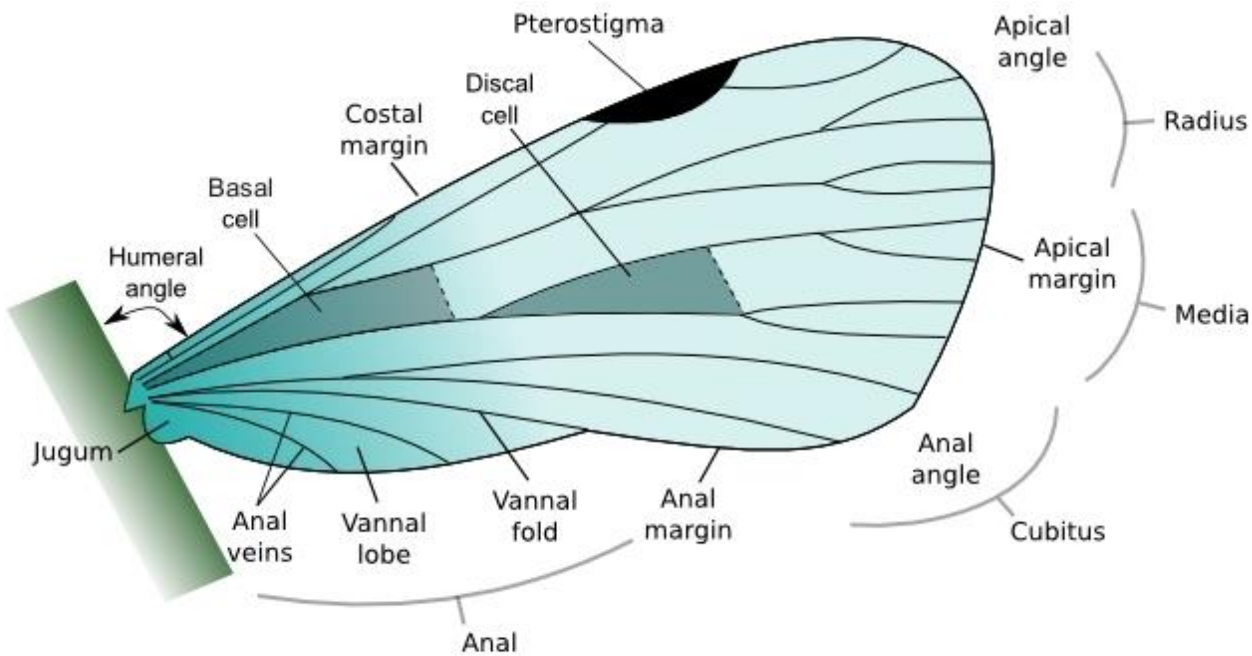


Fig 2.4 Structure of a typical Wing.

2.4.1 TYPES OF WINGS

1. Terminal: (Singular: Tegmen):

Wings are leathery or parchment like. They are protective in function. They are not used for flight. E.g. Forewings of cockroach and grasshopper.

2. Elytra (Singular: Elytron):

The wing is heavily sclerotized. Wing venation is lost. Wing is tough and it is protective in function. It protects hind wings and abdomen. It is not used during flight but during flight they are kept at an angle allowing free movement of hind wings, e.g. beetlesandweevils.

3. Hemelytra (Singular: Hemelytron):

The basal half of the wing is thick and leathery and distal half is membranous. They are not involved in flight and are protective in function, e.g. Fore wing of heteropteran bugs.

4. Halteres: (Singular: Haltere):

In true flies, the hind wings are modified into small knobbed vibrating organs called halteres. Each haltere is a slender rod clubbed at the free end (capitellum) and enlarged at the base (scabellum).On the basal part, two large groups of sensory bodies forming the smaller hick's papillae and the large set of scapel plate. They act as balancing organs and provide the needed stability during flight, e.g. true flies, mosquito, male scale insect.

5. Fringed wings:

Wings are usually reduced in size. Wing margins are fringed with long setae. These insects literally swim through the air, e.g. Thrips.

6. Scaly wings:

Wings of butterfly and moths are covered with small coloured scales. Scales are unicellular flattened outgrowth of body wall. Scales are inclined to the wing surface and overlap each other to form a complete covering. Scales are responsible for the colour.

7. Membranous wings:

They are thin, transparent wings and supported by a system of tubular veins. In many insects either forewings (true flies) or hind wings (grasshoppers, cockroaches, beetles and earwigs) or both forewings and hindwings (wasps, bees, dragonfly and damselfly) are membranous. They are useful in flight.

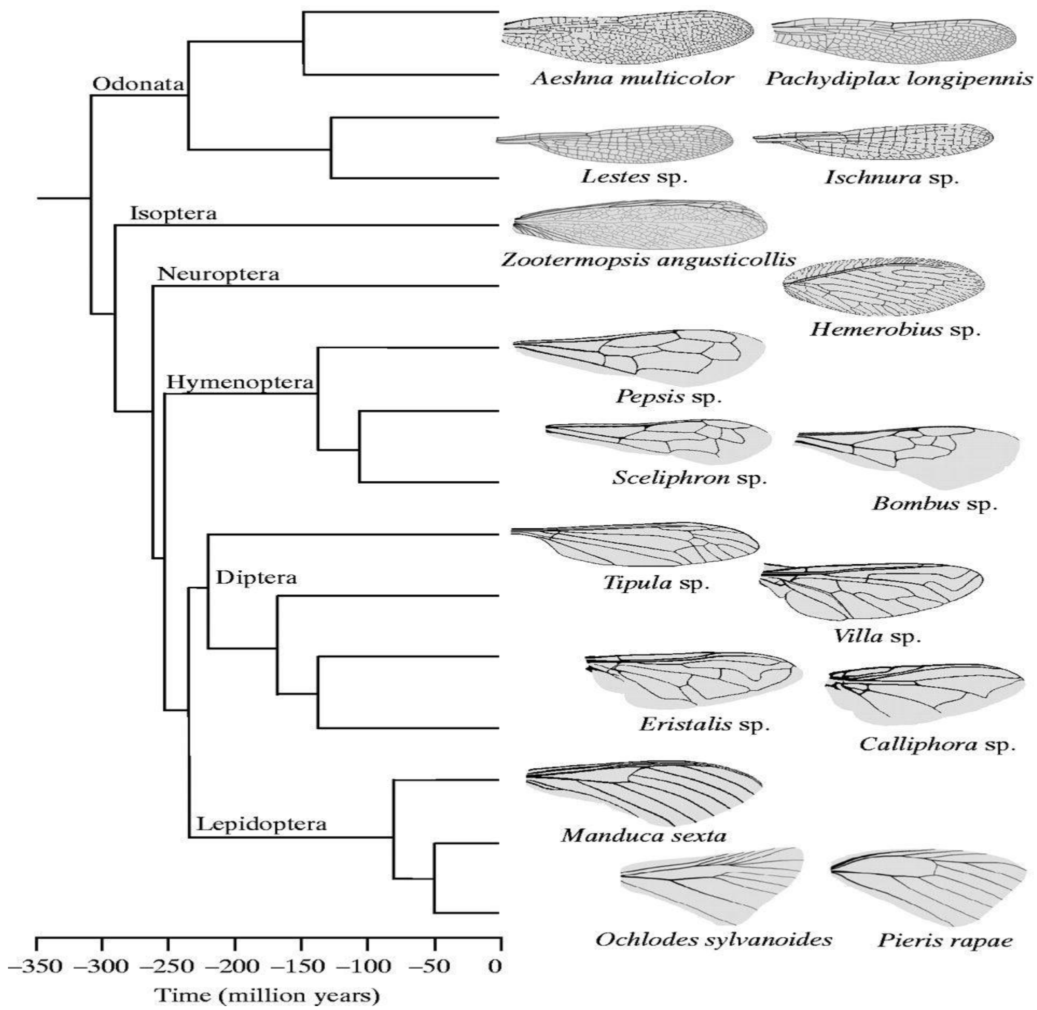


Fig 2.5 Types of Wings of insects.

2.4.2 HYPOTHETICAL WING VENATION

The wing regions and basement of the insect.The margins of wings are named as the anterior margin and posterior margin. In the order Diptera, a pair of membranous lobes at posterior margin of the wing base is predominantly evident and is known as the outer and inner squamma.

The wings are well-developed in the housefly. They include the tegula, the axillary cord, axillary sclerites and variable form of skeletal plate. The tegula are mostly confined to the forewings, particularly in the orders Lepidoptera, and Diptera, each lies at the base of the costal vein as a small hairy chitinous pad of dorsal side of insect. There are three axillaries at the base of wing. The second axillary lies at the base of radius vein and articulate with the first axillary proximally and with the wing process of the pleuron end. Third and fourth articulate directly, connect with the posterior notal wing process. It is in present in the order Orthoptera.

Generally, in all the insects, there are some similarities in the wing venation and therefore, it is presumed that all types of wing venations have developed from the common base or the same ancestor. Accordingly, we say primitive wing venation has developed from two tracheae, which are situated on the anterior and the posterior basal margins of the wing and their branches are spread all over the wing. Each main trachea gives rise to three principal veins, thereby forming six principal veins namely costa, radius, medius, and cubitus, penultimate and ultimate. Each principal vein gives rise to a sub-vein near its base. The principal veins are denoted by + sign and sub vein represented by – sign.

Thus, the whole wing venation system is represented by + and – signs. Such type of hypothetical wing venation in never met in any insect, as one or the other vein is invariable found lacking for example the medius vein is absent in some insects, like in order Hemiptera, Odonata, etc. Due to unique distribution of longitudinal and cross veins, the wing becomes divided into a large number of small spaces. They can be divided into two type’s basal cell lying towards the base of wings and the distal cells lying in between the branches of principal veins. The venation of wing is greatly modified in different groups of insects.

2.4.3 WING COUPLING MECHANISMS

Cross veins and wing coupling apparatus: The veins joining the two longitudinal veins are known as cross veins. The important cross veins have many types such as (i) humeral cross vein (ii) Radio-medial cross vein (iii) Medial cross vein (iv) medio -cupital cross veins and (v) Radial cross vein.

The wing coupling is done mostly with the help of lobes or spines lying at the wing and a humeral lobe at the base of costal margin of hind wing. Both lobes contain setae. The humeral lobe especially bears the frenular bristles. From this primitive type of wing coupling mechanism, complex types have been evolved.

Other insects have the wings coupled by more distal modification, which hold the costal margin of the hindwing to the anal margin of the forewing. Thus, Hymenoptera and Heteroptera have a row of hooks, the hamuli, along the costal margin of the hind wing catch into a fold of the forewing. Thus,synchronous action of the fore and hind wings, thereby enabling the insects to fly more swiftly. Types of various coupling apparatus are: Jugal and Humeral lobe, frenulum and Retinaculum and Hamuli.

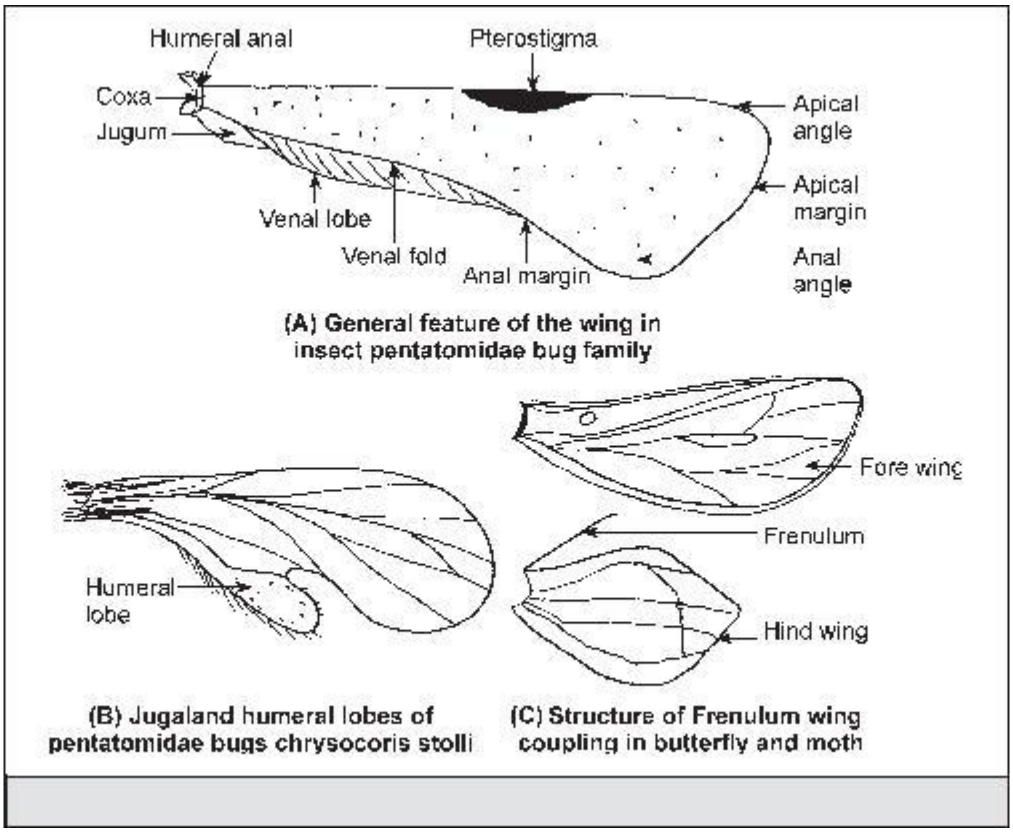


Fig 2.6. Mechanism of Insects wing.

2.4.4 FLIGHT MECHANISM OF INSECTS

In order to fly, there are a few important factors:

1. The shape of the wings.
2. The ability to move it through the air.

3. Scientists have been trying to work out how insects fly for many years. This has been quite tricky due to the size of the insects - very tiny - and the speed at which they fly around. Have you tried to follow a fly or a wasp around the house to try to open the correct window to let it out? They seem to disappear and then all of a sudden it is right beside you! When high-speed film was invented this made the scientist life so much easier and started to give them all the information they were missing. What has been found out is that insects use two different mechanisms for flying - either indirect mechanism or direct mechanism.

Direct Flight Mechanism

This involves the insect using the muscles that attach the wings to their bodies to move their wings first in one way such as up and then the other way down but sometimes this is sideways and backwards and forwards - quite a complicated movement.

Indirect Flight Mechanism

This is slightly different as instead of just moving the wings by way of muscle sets, they change the shape of the thorax, the center part of the insect's body almost like when we breathe in and out and change the shape of our chest and stomach. This mechanism moves the wings sounds exhausting for a wee tiny insect but actually uses less energy than the direct flight.

(**https://www.woodlandtrust.org.uk/**)

2.4 SUMMARY

The thorax is the middle body part to which the legs and wings are attached. Insect legs are typically 6-segmented (coxa, trochanter, femur, tibia, tarsus, pretarsus) usually having only one trochanter and lacking a patella. The abdomen contains digestive and reproductive organs internally and often reproductive structures externally. The sides of both the thorax and the abdomen are lined with tiny openings called spiracles, through which an insect obtains oxygen. The margins of wings are named as the anterior margin and posterior margin. In the order Diptera, a pair of membranous lobes at posterior margin of the wing base is predominantly evident and is known as the outer and inner squama. Generally, two pair of wings are present which are the out growths of the body wall along the lateral margin of thorax. The presence of wings is one of the most characteristic features of the insect and provides one of the most useful Taxonomic aids of insects.

2.6 TERMINAL QUESTIONS AND ANSWERS

1. Explain different types of insect legs.
2. Describe different types of insect wings.

REFERENCE

- P.K.Sehgal, (2017).Fundamental of Agricultural Entomology, first edition, Kalyani publishers New Delhi. Pp1-399.

UNIT 3:ABDOMEN OF INSECTS

3.1 Objectives
3.2 Introduction
3.3 Structure of Genitalia
3.3.1 Male Genitalia
3.3.2 Female Genitalia
3.4 Summary
3.5 Terminal Questions and Answers

3.1 OBJECTIVES

The unit describes the characteristics of the phylum Arthropoda and the all classes contained in the phylum.It has a detail information on the class Insecta and 29 orders. At the end of this unit you should be able to differentiate between all the orders of class Insecta. This unit gives an account of various segments of the body of the insects. It introduces the reader to various appendages found on the head and thorax of the insect. By the end of this unit you will be able to describe the various modification of legs and wings of the insects. The three main insect body parts are *head, thorax,* and *abdomen.* The head contains the antennae, eyes, and mouthparts. The thorax is the middle body part to which the legs and wings are attached. The abdomen contains digestive and reproductive organs internally and often reproductive structures externally. The sides of both the thorax and the abdomen are lined with tiny openings called spiracles, through which an insect obtains oxygen.

3.2 INTRODUCTION

Arthropoda is a largest phylum of animal kingdom.It includes about 1,13,40,000 species in all habitats.This constitutes about 83%of all the known animal species on the earth.In Insecta and other arthropods,the body is segmented and each segment basically has a dorsal sclerite (the tergum),joined to a ventral sclerite (the sternum)by the lateral membranous areas,the pleura.In the insects, the segments are grouped into the head,thorax and abdomen, in which the various basic parts of the segments are greatly modified or lost.In the previous chapters, we studied about the head and thorax of the insects. Head is the center for feeding and sensation,where feeding organs and sensory organs are present. This type of grouping of segments into body regions is called tagmosis and each region is called tagmata.Thorax is the center for locomotion.The legs and wings are present on this region, it consists of three segments. Abdomen is the center for digestion and reproduction and consists of 11 segments.Each body segment is found into a ring like structure by the fusion of dorsal tergum, ventral sternum and lateral pleural.

3.3 STRUCTURE OF GENITALIA

Abdomen of Insect: Insect genitalia are complex structures with elements derived from the internal reproductive organs, posterior abdominal segments, and appendages, which may be elaborated or reduced in different groups. Male genitalia consists of the copulatory organ, and in some groups, males possess external claspers the abdomen is generally comprised of 10 rings like segments which are also known as uromeres. They are almost similar in structure except of those on the posterior end, which are highly modified to form the external genitalia. The abdomen of grasshopper consists of 10 segments. The dorsal surface is composed of a thick cuticle layer known as tergum, which form the 2/3 portion of each of the segment and termed as sternum, male and female insects.

3.3.1 MALE GENITALIA

Male -genital organs of insect. The male external genitalia are used in holding the female genitalia for sperm transfer. The principal male genitalia in advanced pterygotes consists of a pair of moveable plates at the ventroposterior surface of ninth segment and are generally called claspers. The inner wall of the distal part of the aedeagus is in continuation of the ejaculatory duct and is called endo phallus.In Thysanura, the genitalia are very simple in structure and the phallus is difference into proximal phallobase and the distal aedeagus. The coxites of the ninth sternum are prolonged in to a pair of appendages with slender, finger like style which form the clasper of insects. In normal condition the sub genital plate presses against the supra and plate and thus closing the end of the abdomen of insect. All these structures constitute a sperm ejection pump in which open the ejaculatory duct on the dorsal side of the Phallobase and important part of insect copulations.

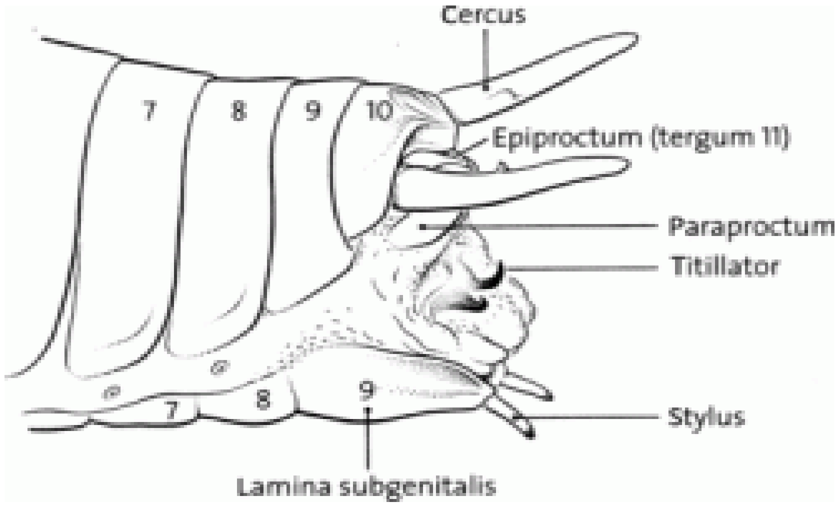


Fig. 3.1 Male genitalia of grasshopper.

3.3.2 FEMALE GENITALIA

Grasshopper 9th and 10th abdomen alternates are so closely united that they appear to be one segment. In the generalized female pterygotes, insect family pentatonic, modified him eighth and ninth abdominal segment appendages of form the ovipositor or egg-laying apparatus, which are composed of two pairs of basal valvifers. The female gonopore is usually on the posterior to the eightabdominal segment. The male external copulatory organs penis-aedeagus is usually borne on the ninth abdominal segment.

The female Genital Organs of Insect. The genital of female grasshopper consists of a copulatory pouch and a special egg laying organ known as ovipositor. These organs are considered to be the appendage of 8th and 9th abdominal segments. The ovipositor helps to the female in depositing her eggs in the soil by digging hole in the ground. The inner valves are considered to be vestigial and non-functional where the dorsal and ventral valve fit together to from the functional ovipositor. There are three pairs of valves, which collectively form the ovipositor. The first pair originates from the 9th sternum which is triangular pointed and hard in structure known as dorsal valves.The second pair of ventral valves originating from the 8th sternum, which is similar to dorsal valve and projected up and down and a 3rd pair of valves lying in between the dorsal and ventral valves known as inner valves.

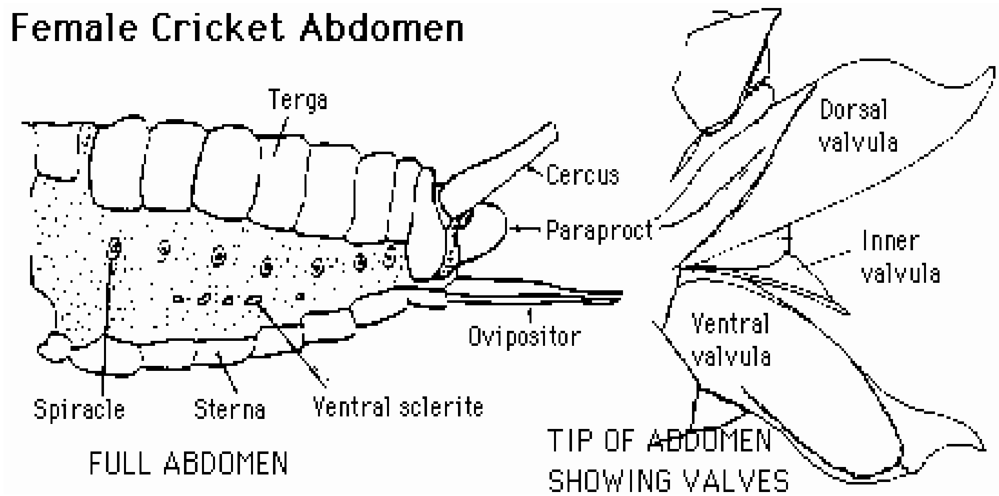


Fig 3.2 Female genitalia of grasshopper.

3.4 SUMMARY

The abdomen contains digestive and reproductive organs internally and often reproductive structures externally. The sides of both the thorax and the abdomen are lined with tiny openings called spiracles, through which an insect obtains oxygen. This type of grouping of segments into body regions is called tagmosis and each region is called tagmata.Thorax is the center for locomotion.The legs and wings are present on this region. It consists of three segments. Abdomen is the center for digestion and reproduction and consists of 11 segments.Each body segment is found into a ring like structure by the fusion of dorsal tergum, ventral sternum and lateral pleural. Insect genitalia are complex structures, with elements derived from the internal reproductive organs, posterior abdominal segments, and appendages, which may be elaborated or reduced in different groups. Male genitalia consist of the copulatory organ, and in some groups, males possess external claspers the abdomen is generally comprised of 10 rings like segments which are also known as uromeres. All these structures constitute a sperm ejection pump in which open the ejaculatory duct on the dorsal side of the Phallobase and important part of insect copulations. The genitalia of female consists of a copulatory pouch and a special egg laying organ known as ovipositor. These organs are considered to be the appendage of 8th and 9th abdominal segments. The ovipositor helps to the female in depositing her eggs. The inner valves are considered to be vestigial and non-functional where the dorsal and ventral valve fit together to from the functional ovipositor. There are three pairs of valves, which collectively form the ovipositor.

3.5 TERMINAL QUESTIONS AND ANSWERS

1. Describe the male genital organsof any insects.
2. Explain the reproductive organs of any insects.

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UNIT 4: DIGESTIVE SYSTEM

CONTENTS:

4.1 Objectives

4.2 Introduction

4.3 Structure and modification of alimentary canal in insect

4.4 Food and feeding mechanism

4.5 Digestion in different insect

4.6 Absorption

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4.8 Nutritional requirement

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4.10 Endosymbionts

4.11 Summary

4.12 Terminal Questions and Answers

4.1 OBJECTIVES

After studying this unit, the students will be able to learn and acquire knowledge about

- The structure and modification of alimentary canal
- Process of digestion in different insect
- Mechanism of feeding and food habitat
- Nutritional requirement of insect
- Ectosymbiotic and endosymbiotic fungi association with insect

4.2 INTRODUCTION

In insects, complete digestive system is found. Diversity of insect shows different modification of alimentary canal. Insect uses its digestive system for digestion of food. Digestion is a biological process in which breakdown of complex molecule into simpler form. The food enters through mouth and then processed with the help of enzymes. The undigested food eliminates through anus. Digestive system composed of alimentary canal and associated glands. In insect,the alimentary canal is divided into foregut, midgut and hind gut. In Diptera, the peritrophic membrane is present, which protects the midgut. This membrane is made up of chitin. In fluid feeding insects, such as, Lepidoptera, the filter chamber is present by which water passes directly from midgut to hindgut. In cockroach, 7to 8 hepatic caeca are present which produces digestive juices. The hindgut is a last part of alimentary canal and has three regions, viz. ileum, colon and rectum.

In mouth region, the salivary gland is present which contains enzymes, like amylase and invertase that help in digestive process. The main group of enzymes are carbohydrases, lipase, protease, exopeptidase and endopeptidase. The nutrition provided dietary requirement. Insect has nutritional needs, as well as feeding behaviour associated with obtaining food. Insects eat to satisfy their nutritional needs, as well as the feeding behaviour and sensory physiology. Micronutrient like sterols, vitamin and some mineral are required in small but other phytosterol and ergosterol from fungi. Vitamin required for growth in insects. Water- and fat-soluble vitamins are present in the insects. Some act as cofactors, such as vitamin B. In insects, the moulting process occur with the help of vitamin C. Ectosymbiosis is a type of symbiotic behaviour, which is found in many diverse species. Symbiotic association provide by both parasite and host mutually. Parasites live on body surface of host and some lived internally, such as in glands and lining of digestive tube. Laboulbeniomycetes is a group of fungi and a member of ascomycetes. These fungi grow on different anatomical part of insects.

4.3 STRUCTURE AND MODIFICATION OF ALIMENTARY CANAL IN INSECTS

The alimentary canal of insects is along, muscular, and tubular structure extending from mouth to anus. It is divided into three main regions: the foregut or stomodeum, which is ectodermal in origin; the midgut or mesenteron, which is endodermal; and the hindgut or proctodeum, which again is ectodermal. All parts of the gut epithelium consist of a single layer of cells. Foregut and hindgut are ectodermal in origin, the cells secrete cuticle, which is continuous with that covering the outside of the body. The lining cuticle is known as the intima. It is shed and renewed at each molt. Although, the midgut does not secrete cuticle, in most insects, it does secrete a delicate peritrophic envelope around the food. Phytophagous insects have longer alimentary canal than carnivorous insects and insect feeding on a largely protein diet have shortened gut than those feeding on carbohydrates.

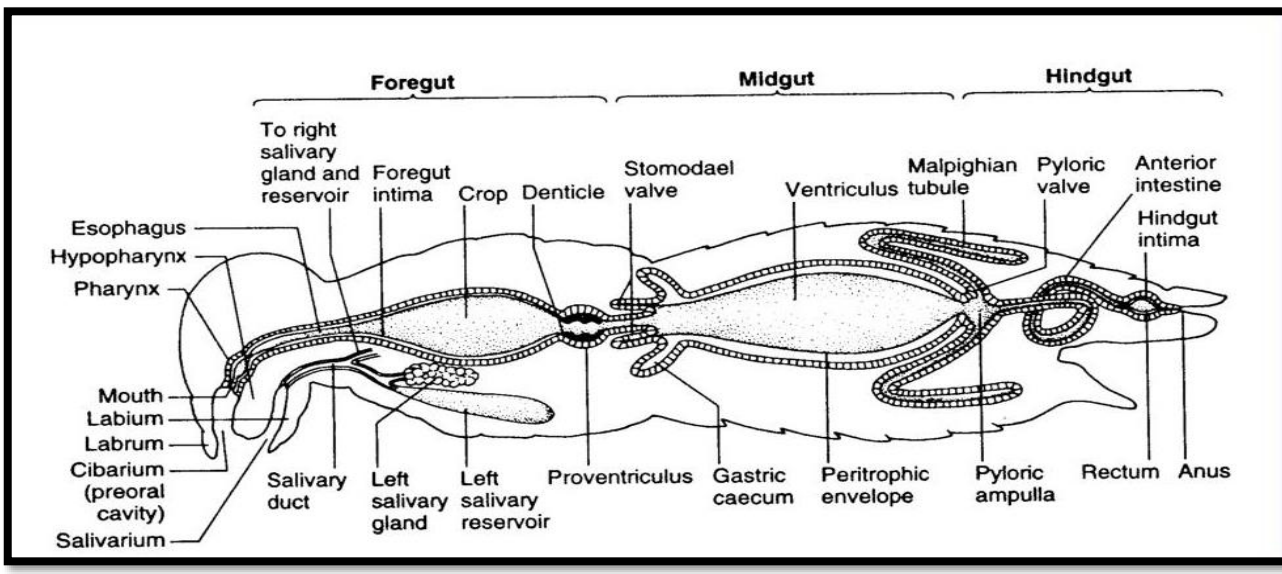

Fig4.3a. Digestive system of insect.

Usually, the gut is a continuous tube running from the mouth to the anus, but in some insects that feed on a fluid diet containing little or no solid waste material the connection between the midgut and the hindgut is occluded. This is the case in some plant-sucking Heteroptera, where the occlusion is between different parts of the midgut, and in larval Neuroptera, which digest their prey extra-orally. In these insects a pellet of fecal matter is deposited at the larva–pupa molt.

I. FOREGUT

Foregut is ectodermal in origin. It consists of mouth, pharynx, oesophagus, crop and gizzard or proventriculus. Invagination of ectoderm forms foregut (Stomodeum).

Mouth: Terminal mouth parts leads into a preoral cavity. Preoral cavity between epipharynx and hypopharynx is called as Cibarium. Preoral cavity between hypopharynx and salivary duct is Salivarium. In cockroach, mouth is surrounded by mouth parts.

Pharynx: - A musculated organ called pharynx is present behind the mouth which drives the food into esophagus. It is short and tubular. It has a sequence of dilator muscles inserted into it. In sap feeders, pharynx acts as a pharyngeal or sucking pump.

Oesophagus: It is a short narrow tube whose function is to passes food from pharynx to crop. Crop acts as food reservoir. In bees, the crop is called as honey stomach where nectar conversion occurs.

Gizzard: Crops open into small cone shaped, muscular and thick-walled chamber called gizzard. It is the posterior part of foregut. It is present in solid feeders and absent in fluid feeders or sap feeders. It is variously modified in different insects. In cockroaches, which feed on solid food material and cuticle develops six strong plates or teeth, whose function is to grind the food. It controls the passage of food from the crop to the midgut.

II. MIDGUT

Midgut is the middle part of the alimentary canal. It is endodermal in origin and is also called as mesenteron. It is internally lined by glandular epithelium and it works for digestion and absorption. Midgut is short narrow tube like part known as mesenteron and ventriculus. It is composed of secreting and absorption epithelium. Midgut is made up of three types of epithelial cells. (i) Secretory cells (ii) Goblet cells (iii) Regenerative cells which replaces secretory cells. Main structures present in midgut are as follows:

i) **Peritrophic membrane**: The epithelial cell of midgut is protected by peritrophic membrane. It serves as a physical barrier between gut content and midgut epithelia found in most insects. It is present in solid feeders and absent in sap feeders. It lubricates and facilitates the food movement.The peritrophic membrane protects the midgut cells from abrasion by food and helps compartmentalize the food for digestion, and serves as an innate defense against viruses and other microbial pathogens. Peritrophic membrane (PM) is a film that surrounds the food bolus in most insects. PM is composed of chitin and proteins. Peritrophic membrane proteins (PMPs) are composed of one to several chitin-binding domains (CBDs), which may include mucin-like domains.The six-cysteine motif is also found in several peritrophic matrix proteins, as well as in receptors and other proteins that are involved in cellular adhesion.

According to modes of formation, two types of peritrophic membrane are recognized. In Diptera, single layered membrane is secreted as a viscous fluid at the anterior end of midgut. This fluid is forced through a pressure formed by the stomodeal invagination so that it forms a tube which becomes a membrane. Second type of membrane is formed by delamination from the whole surface of the midgut. It occurs in Orthoptera, Odonata, Coleoptera, and Hymenoptera. It protects the cells from damage by the gut contents. It acts as a barrier to microflora so that infection is prevented, while in fluid feeder it helps in absorption. It is permeable to enzymes and product of digestion.

(ii) Gastric caecae or Hepatic caecae

Hepatic caeca is found between the junction of foregut and midgut in insects. They are producing digestive juices. Hepatic caeca increases the functional area of midgut and it also housing the symbiotic bacteria in some insect. In cockroach 7 to 8 hepatic caeca are present.

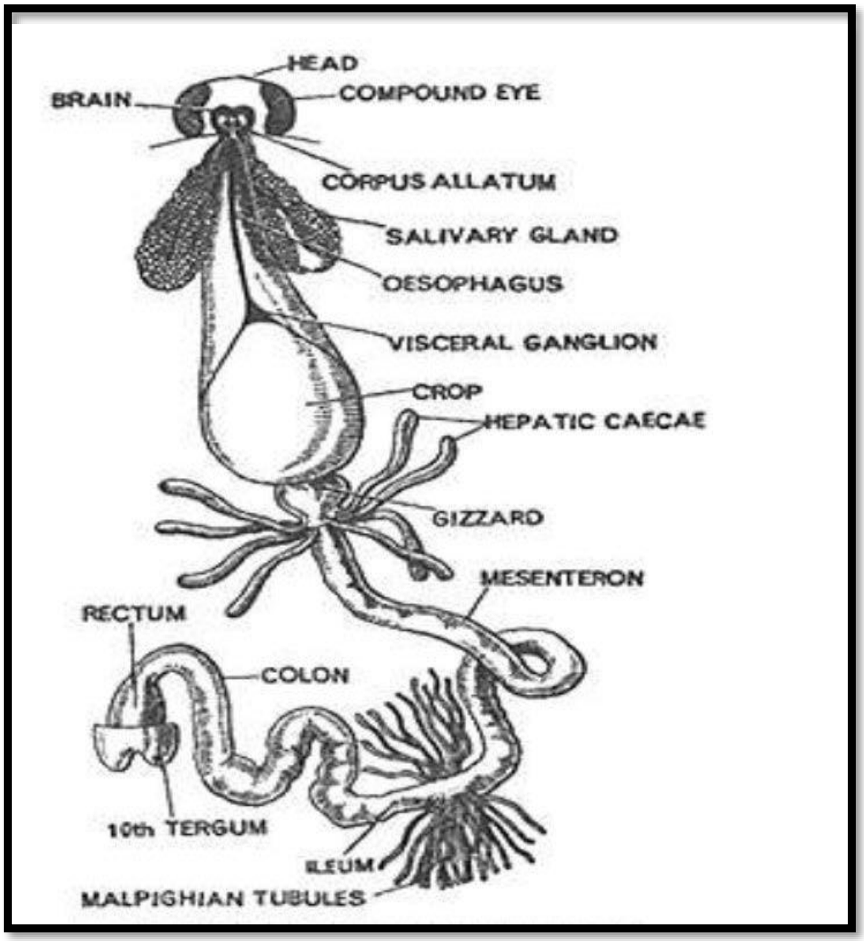

Fig.4.3b: Alimentary canal of cockroach.

(iii) <u>Filter chamber</u>:

Insects that feed on plant sap like leaf hopper and aphids must process large volumes of liquid in order to extract enough protein to meet their metabolic needs. A filter chamber mechanism allows excess of water and sugar to bypass most of the insect's digestive system for excretion as honey dew. In fluid feeding insects, such as a Lepidoptera, Homoptera and some Heteroptera. In these insects, the fluid is absorbed, which then passes into blood and then excreted by the Malpighian tubules. These insects ingest large quantities of liquid food, so that modification of gut takes place, which provide rapid elimination of excess of water. This is necessary to avoid excessive dilution of haemolymph and to concentrate the food for enzymatic activity. By filter chamber, water passes directly from the midgut to the hindgut along osmotic gradient and there is no significant flow of fluid through the lumen of gut. It is found in Lepidoptera, Hymenoptera and Diptera which feed on nectar.

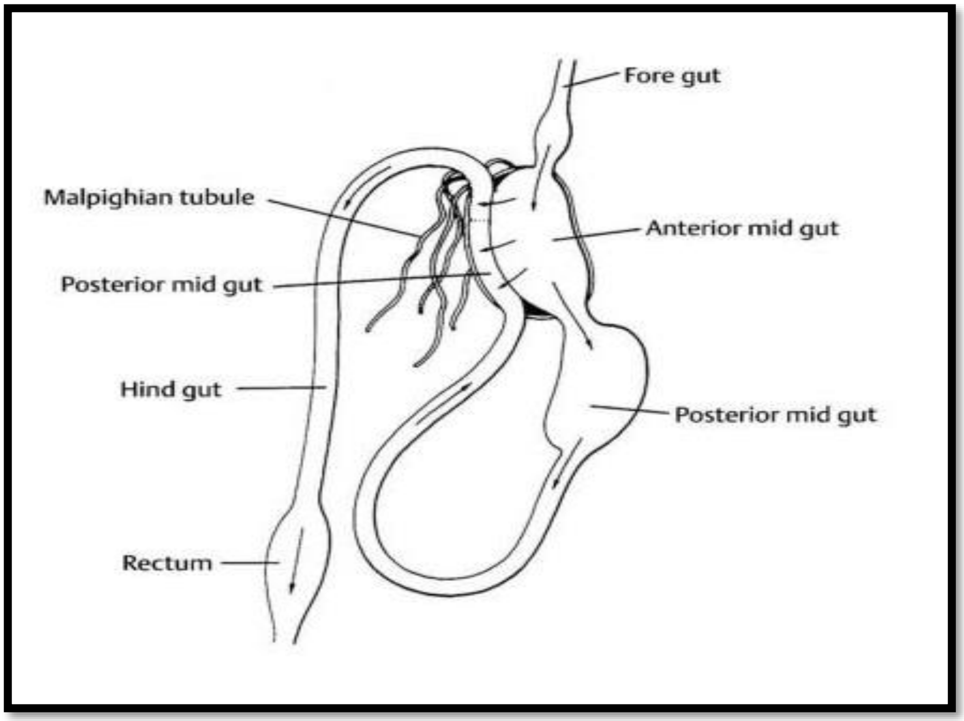

Fig. 4.3c Filter chamber in bug.

III. HINDGUT

Hindgut is the last part of the alimentary canal and is lined internally by a layer of cuticle. It is ectodermal in origin and developed by the posterior invagination of ectoderm. Internal is permeable to salts, ions, amino-acids and water. The main functions of hindgut are the absorption of water, salt and other useful substances from the waste product in alimentary canal. Hindgut is differentiated into three regions:

I) Ileum
II) Colon
III) Rectum

I) **Ileum** –Ileum is absorptive part. It is narrow and short tube known as small intestine. In cockroaches, it bears seven tiny triangular lobes internally bearing spicules and performing as a sort of sphincter. In termite, the protozoa are present here, which helps in the digestion of cellulose.

II) **Colon-**It is longer and wider with an irregular shape.

III) **Rectum-** It is an oval or spindle shaped sac, it bears rectal pads, these are 6 in number and known as rectal gland. These are important in the reabsorption of water, salt and amino acids from urine. In aquatic insects, there are tracheal gills in the rectum. In the larvae of dragonflies, water is pumped in and out of the rectum so that water around the gills is constantly renewed and by the forceful ejection of water insect is able to push itself forward rapidly. Rectum opens outside by anus.

4.4 FOOD AND FEEDING MECHANISM

Insects have different food habitats. Most insects feed on plants including stems, leaves, seeds, and flowers. Such insects are called herbivorous insects. Caterpillars are the most famous herbivorous insects because of the large volume of leaves they consume. Tremendous amounts of leaves eat by caterpillar have significance to prepare for the pupal stage and metamorphosis.

There are many insects that eat fruit including beetles, aphids, butterflies, maggots, hornets, wasps and some flies. These insects often feed on very ripe or decaying fruits. Fruit provides insects with an excellent source of carbohydrates and other nutrients.

There are also some very interesting mutualistic relationships between insects and plants. Mutualism is when both organisms of different species benefit from the relationship. An example of a mutualistic relationship is that between ants and acacia plants. The acacia plants provide the ants with shelter and protection inside the plant's thorns. The ants provide the acacia plant with protection from other herbivores. The ants also trim back the leaves of other plants blocking sunlight from the acacia.

Carnivorous insects are those that have a diet including meat. Some carnivorous insects eat other insects, some drink blood, and some eat decaying animal flesh. Dragonflies are almost exclusively carnivorous and usually eat butterflies, smaller dragonflies, midges, moths, and mosquitos. Another carnivorous insect is the Hawaiian caterpillar. These caterpillars use silk traps to capture slugs.

Animal feces, is a common food source for many insects. Some dung beetle, called rollers, collect fecal matter by rolling it into a large ball. They use this ball of dung for food as well as a breeding chamber. Other dung beetles, called tunnelers, find dung and bury it before returning to eat. Tunnelers can bury up to 250 times their weight in dung in a single day. Several types of flies also feed on animal dung.

There are five modification and mechanism of feeding associated with organisms. These feeding mechanisms include:

1) Biting and chewing mechanism- This type of feeding mechanism is seen in grasshoppers and cockroaches. Their mouth parts adapted for biting and chewing. These mouth parts are:

i) **Mandibles** – These are toothed and jaw like structure used for chewing and cutting food. The biting surface is differentiated into proximal molar or grinding region and more distal incisor region or cutting region. In pterygotes, the mandibles are articulated with the cranium at two points with head capsule and subgenae.

ii) **Labrum-** Labrum is also called upper lip. It prevents food from dropping of mouth. On its inner side, it is membranous and may be produced into medial lobe called epipharynx, the labrum is raised away from mandibles by two muscles arising in the head; it is closed against the mandibles by two or more muscles, which are attached to the sclerites called tormae. These muscles can produce a lateral rocking movement of the labrum.

iii) **Labium**- The labium or lower lip prevent wastes of food from mouth. It is formed by the fusion of a pair of maxillae like appendages, commonly called lower lip and it encloses the mouth from lower or behind. The basal part of the labium is called postmentum. This may be subdivided into a proximal submentum and distal mentum. Distal to the postmentum is the prementum. Terminally this bear four lobes.

iv) **Maxillae**- It is present laterally on the head behind the mandibles. A pair of maxillae or biting blade breaks down the food, which the mandibles have chewed into smaller particles. Each maxilla is composed of the following parts-

1) **Cardo**- It is proximal part of maxillae, triangular and attached to the head of capsule by single articulation.

2) **Stipes**- It lies above the cardio and is the central part of the maxillae, stipes contain distally two lobes an inner lacinea and outer galea, on lateral side stipes contain a jointed leg like palp.

3) **Labium-** It is formed by the fusion of a pair of maxillae like appendages, commonly called as lower lip and it encloses the mouth from lower or behind. The basal part of the labium is called the postmentum. This may be subdivided into a proximal submentum and a distal mentum. Distal to the postmentum is prementum. Terminally this bear four lobes, two inner glossae and two outer paraglossae, which are collectively known as ligula. A pair of palps arises laterally from the prementum, often being three segmented.

v) **Hypopharynx-** It is median lobe present behind the mouth. The salivary ducts open behind it and labium. It is fleshy tongue, arising from the floor of mouth or preoral cavity and is usually attached to the inner wall of the labium. Its size and form are quite variable and it is more or less covered with hairs. It functions as a fine tube used for piercing during feeding. So, maxillary palps act as sensory feelers to locate the food. Lacinia are often used for grasping the food and cutting or chewing it. Mandibles masticate with their teeth like process. Ligula formed by paired glossa and paraglossa help in pushing the food into pharynx.

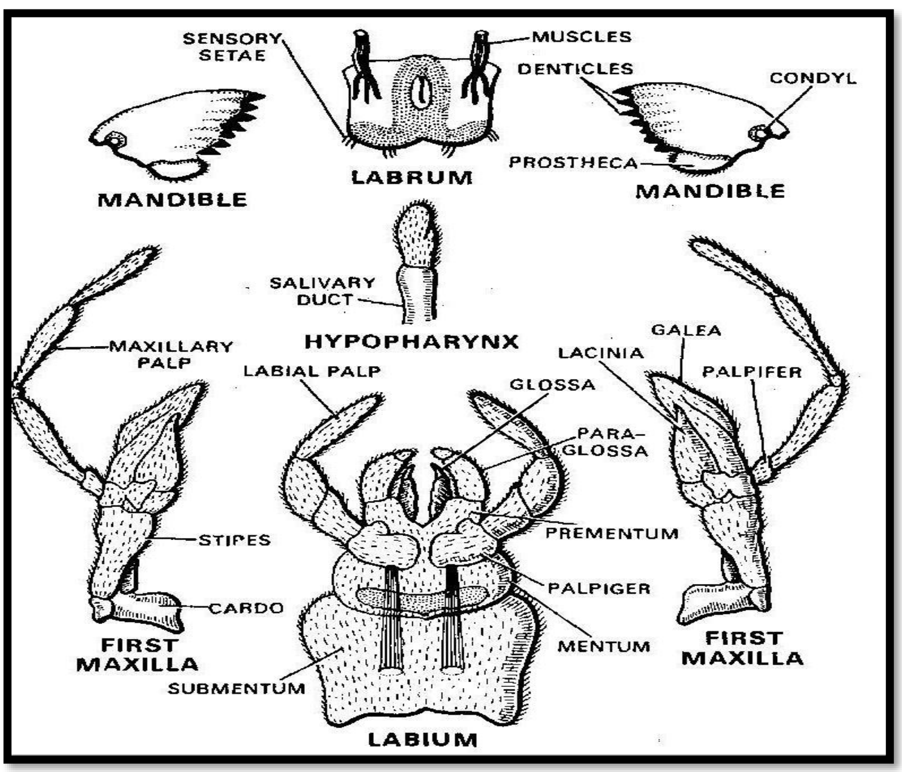

Fig 4.4a: Mouth parts of cockroach.

2) **Siphoning mechanism**– This type of mouth parts is found in the butterflies and moths which feed on the nectar. The long-coiled proboscis is formed by the two galeae of the maxillae. The food channel is between the galeae. The labrum is reduced to narrow transverse band across the lower margin of the face. Mandibles and hypopharynx are absent, but labial palps are usually well-developed. The liquid food is sucked or siphoned up through the proboscis. When the proboscis is not in use, it is coiled and at feeding it become uncoiled due to blood pressure.

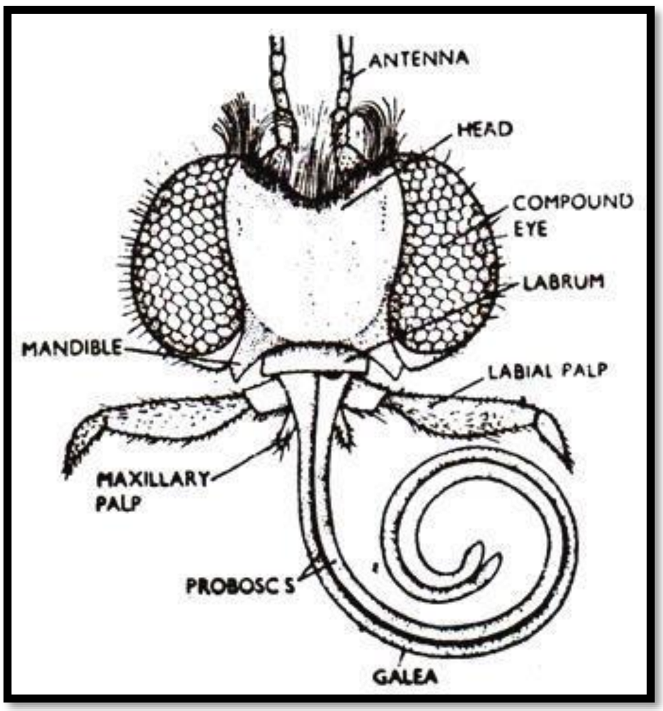

Fig. 4.4b:Mouth parts of butterfly.

3) Sucking mechanism- The mouth parts of insects which feed on fluid are modified in various ways to form tube through which liquid can be drawn and saliva injected. This is due to the elongation of parts and some typical structures are absent. In Diptera,the food canal is found between the labrum and labium. The salivary glands run through the hypopharynx. In addition, the higher Diptera have specialized pseudotrachea in the labium. These are small channels which open to the exterior and pass liquid food to the food channel. Associated with the tube for feeding is the development of pump for drawing up the fluids and salivary pump for injecting saliva. The feeding pump is formed from cibarium, which by extension of lateral lip of mouth. The cibarial muscle from the clypeus enlarge so that a powerful pump is produced. In *Apis,* the galeae and labile palps form a tube round the elongate fused glossal tongue. Insects belonging to ordersHomoptera and Heteroptera have separate food and salivary canal between the opposed maxillae which are styliform.

4) Sponging type- This type of mouth parts is found in housefly, which is adapted for ingesting liquid or the food which is readily soluble in saliva. The mouth parts comprise of a fleshy and retractile proboscis, which is formed by the modification of labrum. Proboscis is fleshy which projects downward from head. The end of proboscis is enlarged bilobed which act as suction pads. They are called labella. Proboscis divided in to three parts:

i) Proximal rostrum

ii) **Middle haustellum** with a mid-dorsal groove serving as food passage and ventral plate called theca.

iii) **Distal labellum** consisting two expanded lobes or labellae under which many tubes are present called pseudotrachea.

The mandibles are absent and maxillae are represented by its palpi that arise at distal end of rostrum. The labrum and hypopharynx are slender and lie in an anterior groove of the labium, which forms the bulk of haustellum. The salivary channel is in the hypopharynx and the food channel lie between the labrum and hypopharynx. At the apex of the labium are labella, which are a pair of large, soft, oval lobes. The lower surface of these lobes bear numerous transverse grooves, which serve as food channel. Labella function as sponging organs and are capable of taking exposed fluids. Thus, labellum is used to lick the food by contractile activity.

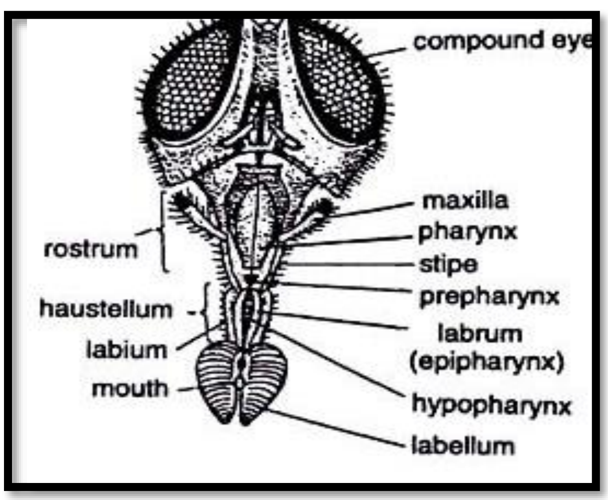

Fig. 4.4c: Mouth parts of housefly.

4.5 DIGESTION

It is a biochemical process in which breakdown of the ingested food into simpler substances and the absorption of the essential nutrients into the body system. Digestion mainly occurs in the midgut, where most of the enzymes are produced.

Digestion are of two types:-

i) Extra intestinal digestion

ii) Internal digestion

i) Extra intestinal digestion- In fluid feeding insects, here enzymes of digestion are present in saliva and digestion often start starts before food is ingested. The enzymes of digestion are injected in to the host or food, in carnivorous insects, the prey is completely histolysed before ingestion.

This type of digestion also occurs in *Dytiscus* larvae, which have no salivary gland so the midgut enzymes are injected into the prey have been digested, the resulting fluid is withdrawn via the same route.

ii) Internal digestion- Most digestion occur in the midgut in which the enzymes are secreted. Some enzymes are regurgitated into crop, so that some digestion also takes place in the crop,*i.e.* in cockroach. In *Schistocerca*, the greatest activity of alpha glucosidase occurs in the lumen of the foregut, caeca, midgut and hindgut also.

In the midgut food is changed into sugar and amino acids by the enzymes of salivary gland and midgut epithelium.

The main group of enzymes are as follows-

1) **Carbohydratases**- These catalyze the breakdown of carbohydrates to simple sugars. Such as-

i) **Amylases**- these act on starch and present in saliva and midgut.

ii) **Glycosidase**- these catalyze the breakdown of complex sugar like maltose, sucrose and lactose into simple sugar.

2) **Lipase**- These catalyzes the breakdown of fat.

3) **Proteases**- These are responsible for digestion of protein, such as-

i) Endopeptidases- Act on protein and peptone and convert them to polypeptide.

ii) Exopeptidase- These digest peptide into amino acid.

Generally, the digestive enzymes in insects are same as found in mammals but pepsin is absent. The type of enzymes depends on the diet, such as cockroaches, which take all classes of enzymes.

Blood sucking insects, such as *Glossina*contains proteolytic enzymes. Butterfly feeds on nectar and contains only invertase enzyme, which digests cane sugar. In termites, the cellulose is digested by protozoans, which are present in the gut. The saliva contains proteolytic enzyme in many flesh-eating insects, both as adults and as larvae. Honey bees have four different types of enzymes, such as inverting sugar for preserving the food in formic acid and for digesting the pollens for the young.

Table 4.1.: Digestive enzymes in insects.

Insect group	**Enzyme**	**Substrate**
Omnivorous insects	Protease	Protein
	Lipase	lipid
Phytophagous larvae	Amylase	starch
	Maltase	maltose
	Invertase	sucrose
Nectar feeders	Invertase	sucrose
Wood boring Cerambycid grub and Termites	Cellulase	cellulose
Meat eating maggots	Collagenase	Collagen and elastin
Bird lice	Keratinase	keratin

Digestion of carbohydrates:

In the midgut epithelium, mostly goblet cells secrete various types of carbohydrate digesting enzymes. These enzymes are called carbohydrates, such as alfa and beta glucosidases, galactosidases, amylases, trehalase, fructosidases, invertase, sucrase, maltase, etc.

Carbohydrates, generally, absorbed as monosaccharide, so that disaccharides and polysaccharides are broken down into monosaccharide. Different enzymes are necessary to hydrolyze different sugars. Initial and intermediate digestion of starch (or glycogen) is accomplished by alpha-amylase. This enzyme cleaves internal bonds of the polysaccharide until it is reduced to small oligosaccharides or disaccharides. Insect amylases depend on calcium ions for activity or stability, they are activated by chloride ions (amylases in Lepidoptera are exceptions), their molecular masses are found in the range 48 to 68 kDa, and their pH optimal vary widely (4.8-9.8) depending on the insect taxon.

The final digestion of starch chains occurs under alpha-glucosidases, enzymes that sequentially remove glucosyl residues from the non-reducing ends of short oligomaltosaccharides. If the saccharide is a disaccharide, it is named maltose. Because of that, alpha-glucosidase is also called maltase. The important insect hemolymph and fungal sugar trehalose is hydrolyzed only by the specific enzyme trehalase. This digestive enzyme occurs in luminal contents or immobilized at the surface of midgut cells and also as an enzyme at the midgut basal cell membrane, making available glucose from hemolymph trehalose.

Although cellulose is abundant in plants, most plant-feeding insects, such as caterpillars and grasshoppers, do not use it. Cellulose is a non-ramified chain of glucose units linked by P-1, 4 bonds arranged in a crystalline structure that is difficult to disrupt. Thus, cellulose digestion is unlikely to be advantageous to an insect that can meet its dietary requirements using more easily digested food constituents. The cellulase activity found in some plant feeders facilitates the access of digestive enzymes to the plant cells ingested by the insects. True cellulose digestion is restricted to insects that have, as a rule, nutritionally poor diets, as exemplified by termites, wood roaches, and cerambycid and scarabaeid beetles. There is growing evidence that insects secrete enzymes able to hydrolyze crystalline cellulose, challenging the longstanding belief that microbial symbionts are necessary for cellulose digestion. The end products of cellulase action are glucose and cellobiose.

Digestion of protein

Initial digestion of proteins is carried out by proteinases (endopeptidases), which are enzymes able to cleave the internal peptide bonds of proteins. For this, different endopeptidases are necessary, because the amino acid residues vary along the peptide chain. Proteinases may differ in specificity toward the reactant protein (substrate) and are grouped according to their reaction mechanism into the subclasses serine, cysteine, and aspartic proteinases. Trypsin, chymotrypsin, and elastase are serine proteinases that are widely distributed in insects and have molecular masses in the range 20–35 kDa and alkaline pH optima. Trypsin preferentially hydrolyzes (its primary specificity) peptide bonds in the carboxyl end of amino acids with basic R groups (Arg, Lys); chymotrypsin is preferential toward large hydrophobic R groups (e.g., Phe, Tyr), and elastase toward small hydrophobic R groups (e.g., Ala). The activity of the enzymes also depends on the amino acid residues neighboring the bond to be cleaved. This may explain the differences in susceptibilities of insects to strains of *Bacillus thuringiensis*, because the harmful effects depend on the previous proteolysis of the bacterial endotoxin. Also, insects fed on trypsin inhibitor–containing food may express new trypsin molecules insensitive to the inhibitors, due to changes in their primary specificities or binding properties of their subsites.

Cysteine and aspartic proteinases are the only midgut proteinases in hemipterans, and they occur in addition to serine proteinases in cucujiformia beetles. Their occurrence in Hemiptera is interpreted as a consequence of the loss of the usual digestive serine proteinases associated with the adaptation of hemipteran ancestors to a diet usually lacking proteins (plant sap), followed by the use of lysosome-like enzymes in adapting to a new predatory habit. The presence of cysteine and aspartic proteinases in cucujiformia beetles is likely an ancestral adaptation to circumvent proteolytic inhibition caused by trypsin inhibitors in ingested seeds. Cysteine and aspartic proteinases have pH optima of 5.5–6.0 and 3.2–3.5 and molecular masses of 20–40 kDa and 60–80 kDa, respectively. Because of their pH optima, aspartic proteinases are not very active in the mildly acidic midguts of Hemiptera and cucujiformia beetles, but are very important in the middle midguts (pH 3.5) of cyclorrhaphous flies.

Intermediate digestion of proteins is accomplished by exopeptidases, enzymes that remove amino acids from the N-terminal (aminopeptidases) or C-terminal (carboxypeptidases) ends of oligopeptides (fragments of proteins). Insect aminopeptidases have molecular masses in the range 90–130 kDa, have pH optima of 7.2–9.0, have no marked specificity toward the N-terminal amino acid, and are usually associated with the microvillar membranes of midgut cells. Because aminopeptidases are frequently active on dipeptides, they are also involved in protein-terminal digestion together with dipeptidases. Aminopeptidases may account for as much as 55% of the midgut microvillar proteins in larvae of the yellow mealworm, *Tenebrio molitor*. Probably because of this, in many insects, aminopeptidases are the preferred targets of *B. thuringiensis* endotoxins. These toxins, after binding to aminopeptidase (or other receptors), form channels through which cell contents leak, leading to insect death. The most important insect carboxypeptidases have alkaline pH optima, have molecular masses in the range 20–50 kDa, and require a divalent metal for activity. They are classified as carboxypeptidase A or B depending on their activity upon neutral/acid or basic C-terminal amino acids, respectively.

Digestion of Lipids

Many insects produce lipases, which hydrolyze fats to fatty acids and glycerol. Larva of wax moth digests the beeswax. Honey comb is the diet of these larvae. Bee wax, from which honey comb is made, is a mixture of esters, fatty-acids and hydrocarbons. Some bacteria also help in digestion of lipids. The comparison of the ability of plant-feeding insects to utilize dietary triglycerides vs. the more polar plant lipids suggests that polar lipids may be significant nutrients for some insects. Both triglycerides and phospholipids have been shown to be hydrolyzed in the intestinal lumen of insects, but the rate of hydrolysis differs among different lipids. Mechanisms for the intestinal emulsification of lipids are not understood well in insects. The lack of endogenous emulsifiers may contribute to the relatively inefficient hydrolysis of triglycerides in some insects in comparison to mammals. Diglycerides have been suggested as key intermediary metabolites in glyceride translocation across the insect gut wall.

Digestive gland

In insects, there are four pairs of glands associated with mouth. The mouth parts associated with these glands are mandibular, maxillary, hypopharyngeal, and labial glands. In holometabolous insect, the gland may be present in only one life stage. In Lepidoptera, mandibular gland present in larval stage only not in adult stage.

(a) Salivary glands

In cockroach, a pair of labial glands function as a salivary gland where the salivary ducts open into the salivarium. In caterpillars, the salivary glands are adapted for silk production whereas mandibular glands function as to produce saliva.

Functions of saliva

- To moisten and to liquefy food.
- To lubricate mouthparts.
- To add taste to gustatory receptors.

- In plant bug saliva contains pectinase which helps in stylet penetration and extra intestinal digestion.
- In gall midge saliva contains Indole Acetic Acid (IAA) which produces galls on plant parts.
- In honey bee saliva contains invertase for sucrose digestion.
- In cockroach the saliva contains amylase for the digestion of starch

(b) Hepatic caecae and midgut epithelial cells

It mainly produces digestive juices. Two types of cells are associated with enzyme secretion.

(i) **Holocrine**: Epithelial cells break down in the process of enzyme secretion.

(ii) **Merocrine**: Enzyme secretion happens without cell break down.

Microbes in digestion

In the insect body, few cells are housing symbiotic microorganisms called mycetocyte. These mycetocytes aggregate to form an organ called mycetome.

(i) Flagellate protozoa – It produces cellulase for cellulose food digestion in termites and wood cockroaches.

(ii) Bacteria – It helps in wax digestion in the wax moth

4.6 ABSORPTION

Insects are the most abundant and diverse class of animals on the planet because of the ability to successfully consume a wide range of foods. Like all heterotrophic organisms, insects need to acquire vital nutrients from their diet. The principal organ for food digestion and absorption of nutrients is the gastrointestinal tract. This organ's principal functions are mediating the efficient digestion of the diet and protecting the organism against harmful chemicals, microorganisms, and mechanical damage from the food.

After digestion of food stuff, in insect’s absorption of nutrients occurs by the process of diffusion which occur through microvilli of midgut epithelial cells. Absorption of water and ions occur through rectum. In cockroach lipid absorption occurs through crop whereas in termites and White grub absorption occurs through ileum. In solid feeders, resorption of water from the faeces occurs in the rectum and the faeces is ejected as pellets. Carbohydrate are generally absorbed as monosaccharide, so that disaccharides and polysaccharide are broken down into monosaccharide.

The evolutionary pattern of digestion and absorption in the midgut which shows a strong phylogenetic influence, modulated by adaptation to particular feeding habits. They recognized basic digestive patterns and were proposed to represent the major ancestors from which the different orders evolved. The recognized ancestors chosen to represent different points in the evolution from basal Neoptera to more derived orders were: Neoptera, Polyneoptera, Hemiptera, Hymenoptera, Diptera, Lepidoptera, and Cyclorrhapha.

4.7 NUTRITION

Insects eat to satisfy their nutritional need, as well as sensory and feeding behavior associated with getting food. For insect nutrition micronutrient are required in small amount. Micronutrient include complex lipid like sterol, vitamins and some mineral.Sterols are essential nutrients for insects in general because they are unable to synthesize them. Sterols play a variety of important roles in insect physiology as components of subcellular membranes, precursors of hormones, constituents of surface wax of cuticle, and constituents of lipoprotein carrier molecules. Insects obtain sterols from cholesterol, but other important sources of sterols include plant phytosterols and ergosterol from fungi. A major dietary component are as follows:

Carbohydrates:

Complex carbohydrates, like starch and glycogen are broken into simple sugars like glucose, galactose or fructose.The role of sugar in insect attack of plants is fascinating. Based on research done on various insect and plant species, apparently insects like moderate amounts of plant sugars and are attracted to plants containing them. But high concentrations of sugars are avoided by leafhoppers, grasshoppers, and the European corn borer. A possible reason that some insects avoid high sugar plants comes from research study. Kreb cycle and oxidative phosphorylation processed these simple sugarsand yield energy in form of ATP. This can be used as a building block for constructing chitin protein. Chitin is a major component of exoskeleton. Insects feed on plant sap must process large quantity of liquid in order to extract enough protein to meet their metabolic need. Termites feed on wood depend on digestive enzymes secreted by protozoa living inside their digestive tract.

Types of carbohydrates:

Polysaccharides: Chitin is a polysaccharide made up of chain of glucose. In insect it is found in exoskeleton. Chitin acts as structural protein.

Oligosaccharides: Common oligosaccharides, viz. maltose, trehalose and sucrose are made up of glucose units.

Simple sugar: The most common simple sugars that make up carbohydrates are glucose, fructose and galactose. Both glucose and fructose are simple sugars and each has the molecular formula: $C_6H_{12}O_6$. These simple sugars contain 6 carbons, 12 hydrogens and 6 oxygens joined together through covalent bond.

Proteins:

Essential amino acids, viz. lysine, tryptophan, histidine, phenylalanine, leucine, isoleucine, threonine, methionine, valine and arginine are present in insect's diet. Protease enzyme break down protein into amino acids. Amino acids used by the cell to make hormones as well as proteins required for muscle, egg yolk, ribosomes and cuticle formation. Some insects digest inert animal protein like keratin and collagen. Tinea (lepidoptera) has keratinase capable of digesting keratin under anaerobic condition. Amino acid can be converted to carbohydrate by removal of amino group and yield energy in form of ATP.

Lipids:

Insects completely depend on lipids for their metabolic needs. In insects, the primary storage organ is fat body. Insects provide high amounts of healthy lipids and low amounts of unhealthy lipids; in other words, they have a high level of omega-3 and a low level of saturated fat. There are differences between the lipid content during the life phases: holometabolous insects, those who have a complete life cycle including larval, pupal, and adult phases, tend to be higher in lipids and lower in protein in their larval stage than in their adult. Lipids make up to 40% of the dry weight of an insect egg, being the most important supply of energy for the developing embryo. Since the oocyte has a very limited capacity to synthesize lipids *de novo*, most of the lipids in the mature eggs arise from the circulation. The main lipid carriers in the insect circulatory system are the lipoproteins lipophorin and vitellogenin. In some species, the endocytosis of lipophorin and vitellogenin may account for about 10% of the lipids present in mature eggs. Thus, most of the lipids are transferred by a lipophorin-mediated pathway, in which the lipoprotein unloads its lipid cargo at the surface of oocytes without internalization. Insects obtained steroid compound from their diet. Hormones and growth factors are formed from steroid. Insects fail to moult into adult stage if taking steroid deficient diet.

Nucleic acids:

Nucleic acids are biological macromolecules. They function in encoding, transmitting and expressing genetic information. Sugar, nucleotide and phosphate are main product of nucleic acid digestion. Coenzymes such as NAD and NADP participate in Krebs's cycle and oxidative phosphorylation. A nucleoside is produced by the hydrolysis of nucleotide play important function in energy exchange with in cell and tissue. ATP provides energy to cell and AMP acts as a secondary messenger that sends information to cell membrane to the cell nucleus.

Beside these above components, insects also obtain vitamins, mineral and water from their food. Insects have ability to synthesize fat soluble vitamin from compound. They also need a dietary source of most water-soluble vitamins. Nerves and muscles need calcium, sodium and potassium. Sulphur plays an important role in both sclerotization of exoskeleton and three-dimensional structure of protein. Most of the terrestrial insects adapted for water conservation and get water from their food. Grain Beetles and flour moth survive by taking small amount of water.

4.8 NUTRITIONAL REQUIREMENT

Insects are notable for their abilities to consume improbable food sources. They are also remarkable for the productivity with each they feed and grow, often on a small amount of food. Insects with distinct larval stages also have the advantage of consuming different food sources, with the larvae avoiding competition with the adults by eating very different food substances, such as, the hungry caterpillar who eats foliage whereas the adult moth or butterfly may feed on nectar. In many cases, the larvae are aquatic and so feed in a very different environment to the terrestrial adults. Cockroaches can live on paper and a little water; silverfish may be kept on nothing more than a small piece of potato. Houseflies, *Musca domestica*, can be grown using meat for their larvae (on which they will lay their eggs) and milk powder and perhaps a little cholesterol, and water for the adults.

A wood-boring insect, *Lyctus,* the powder post beetle, whose larvae bore into wood, leaving behind powdery frass (faeces) of undigested wood. Wood is typically about 50% cellulose (a carbohydrate), 40% lignin and 10% hemicellulose and small amount of starch and other carbohydrates. However, termites have flagellated pro digest particles of wood and break-down the cellulose. The insects can then digest excess protozoa and so derive nourishment. In this way termites will extract much of the cellulose from ingested wood.

Many insects live on low-nitrogen diets, and microorganisms have been suggested to promote insect consumption of these food stuffs in various diverse ways. Some microorganisms simply concentrate the nitrogen. Many microorganisms are valuable to the insect for their wider metabolic capabilities, including their capacity to consume insect nitrogenous waste compounds (e.g. uric acid), synthesize 'high value' nitrogenous compounds (e.g. essential amino acids) and fix nitrogen. Evidence for the microbial utilization of nitrogenous waste products has been obtained for termites, cockroaches and hemipterans.

Insects feeding on cellulose-rich plant materials were once assumed to be 'herbivorous mammals in miniature'. Some termites, such as *Reticulitermes flavipes*were used as examples. *Reticulitermes flavipes*bears a dense community of protists (Oxymonads, Trichomonads and Hypermastigids) that degrade cellulose, yielding short chain fatty acids which are utilized as a carbon source by the insect. Nevertheless, *R. flavipes*is not a miniature mammal because it also has intrinsic cellulases.

Most foods contain compounds (or elements) at concentrations which are potentially deleterious. The hazards are particularly great for herbivores because many plant tissues contain toxic secondary compounds which function as defense against consumers. Insects, like other animals, can protect themselves from such compounds by various routes, including elimination, detoxification and sequestration. These capabilities are generally intrinsic traits of the insect, independent of any microbial associates. The fungus lives on the plant material, detoxifying plant secondary compounds by hydrolases and other enzymes. The fungal mycelium is the only food consumed by ant larvae and also contributes to the diet of adults. In this way, the ants can be considered to exploit the greater detoxifying capability of the fungus to gain access to plant food.

4.9 ECTOSYMBIOTIC FUNGI

Ectosymbiosis is defined as the symbiotic behaviour in which parasites live on the body surface of host. Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: joint-legged invertebrates with a chitinous exoskeleton. The insect cultures the fungi in a special culture medium, such as wood, which is indigestible for the insect. There exists an interdependence between the insect and the fungus, as the latter cannot feed on the wood in the absence of the fungus and the latter cannot exist without the help of the insect. The cultivation of the Ambrosia fungus is known among the termites, ants, wasps and certain wood boring scolytid and platypoid beetles. The fungus growing termite set apart a special compartment in the termitarium for the cultivation of the fungus on a bed excreta. The fungus is used for the reproductive and young forms. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. In a second example, leaf-cutter ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in subterranean gardens. Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also guard their garden, preying on competing fungi. Both ants and fungi benefit from this mutualistic association. The fungus receives a stable supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

Bark beetles belonging to the genus *Dryocoetes* (Coleoptera, Curculionidae, Scolytinae) are known vectors of fungi, such as the pathogenic species *Grosmanniadryocoetidis* involved in alpine fir (*Abieslasiocarpa*) mortality.

The ectosymbiotic community associated with bark and ambrosia beetles is diverse and speciose (rich in species) and adapted for life within tree tissues. This community composed of fungi, bacteria, viruses, nematodes, and mites interacts with beetle hosts in a variety of ways. Interactions are often not simple or clearly understood, and are rather context-dependent, shifting with changing environments. Ectosymbionts also interact with the tree and with natural enemies and competitors of beetle hosts within trees. The effects of changing climate, especially elevated temperatures, on the composition and interactions of the ectosymbiotic community associated with bark and ambrosia beetles.

4.10 ENDOSYMBIONTS

Endosymbiosis is a type of symbiosis in which one organism live inside the other organism. Insects are the most species-rich group of organisms, and it has been estimated that at least 15–20% of all insects live in symbiotic relationships with bacteria. They arose from the arthropod lineage 385 million years (MY) ago and rapidly diversified. The early establishment of symbiotic associations between insects and bacteria about 300million year ago, together with the nutritional enrichment that bacteria offer to insects, could be the key factors in the evolutionary success of this group of organisms. Insect endosymbionts live in a very close environment, inside specialized host cells called bacteriocytes, which may form an organ-like structure (bacteriome) in the body cavity of the insects. The association is obligate for both partners: the bacteria cannot be cultured outside the host, whereas the host needs the bacteria for normal growth and reproduction. In endosymbiosis bacteria, saccharomycetes, flagellates,*etc*. live with in the body of an insect, derive nourishment from it and in turn help digestion of cellulose and other materials for insects. Such type of relationship occurs in many blood sucking insects like *Cimex*, *Glossina*, and *Anopleura*.The symbiotes live free in the adipose tissue, within the gut or in special symbiotic chambers. Larva of lamellicorn beetles have special fermentation chambers, in which cellulose is fermented by bacteria so as to make it easily assimilated by the insect. In *Glossina*, human head lice and pupipara the symbiotes are intracellular with gut tissue.

Termitidae, the rectum is enlarged to accommodate a rich symbiotic fauna of flagellate protozoa belonging to the trichonymphidae and other families. These are able to digest the wood and other cellulose containing material on which the termites feed, producing simple fatty acids which are absorbed and metabolized by the termites. Thus, termite can use cellulose and their diet even in the absence of cellulose digesting enzymes.

Insects are especially susceptible to establishing relationships with intracellular bacteria, including mutualistic endosymbionts. These symbioses are naturally nutritional in nature, and the bacteria often supplement specific nutrients that are missing in the insect host's diet. Such associations are most common among insects that feed on unbalanced diets, such as plant sap, grains, or blood. The majority of recognized intracellular mutualists in insects are found in hosts that feed on plant phloem or xylem sap, including aphids, psyllids, mealybugs, sharpshooters, spittlebugs, cicadas, hoppers, among others. The remarkable ability of these groups to thrive on a sugar-rich but amino acid-poor diet can be reveal by intracellular bacteria that provide essential amino acids and other nutrients. In some cases, two endosymbiotic bacteria inhabit the same host cell and provide a complementary set of nutrients. Insect endosymbionts may also perform more general nutritional functions such as nitrogen recycling, as shown in ants and cockroaches, allowing to access nitrogen during periods of low food input.

Endosymbiosis define medically by various interaction patterns between microorganisms and their residing hosts, best represented by the bacterial endosymbiont. *Wolbachia* identified in arthropods and filarial nematodes, which can affect normal development, reproduction, survival and transmission of the hosts. Based on the transmission modes, vertical or horizontal, and the function of the endosymbionts, the host-symbiont dependence can be divided into primary or secondary. In Dermatology, the role of endosymbionts in skin ectoparasitosis has aroused great interests in the past years. *Riesiapediculicola* is a primary bacterial endosymbiont in body lice *Pediculus humanus*, and supplement their hosts with vitamin B, especially pantothenic acid. In cimicosis, the Gram-negative *Wolbachia* can synthesize biotin and riboflavin, which are crucial for the growth and reproduction of the bedbug *Cimexlectularius*. The high infection rate of adult female ticks *Ixodes ricinus* with the Gram-negative bacteria *Midichloriamitochondrii* present in the mitochondria in diverse ovarian cells, with the high seroprevalence rate in tick-exposed subjects, raises the possibility that this non-pathogenic endosymbiont may play a role in immune response and successful transmission of the tick-borne pathogen.

4.11 SUMMARY

Insects have closed type of digestive system. In process of digestion macromolecules break down into smaller molecules by the assistance of enzyme. The process of digestion occurs in alimentary canal, which is long coiled tube allows the food to enter through mouth and then processed and undigested food eject out through anus. Alimentary canal has three region foregut, midgut and hind gut. Between these region sphincters control the food and fluid movement. Foregut store and grind the food and forward into next region. Midgut produces digestive enzymes. Here, the nutrient absorbed in insect body. Hindgut is divided into ileum, colon and rectum. In this region, absorption of water and salts takes place. Insects also have paired salivary glands. This gland produces saliva to lubricate mouthparts and moisten the food which travels through salivary tubes into mouth. Some microbes are present in few cells of insect are called symbiotic organism that help in food digestion, such as flagellate protozoans produce cellulose for digestion of cellulose in termite.

After digestion of food absorption of nutrients occurs by the process of diffusion which occur through microvilli of midgut epithelial cells. Absorption of water and ions occur through rectum. In cockroaches, the lipid absorption occurs through crop, whereas in termites and white grub absorption occurs through ileum. In solid feeders, the resorption of water from the faeces occurs in the rectum and the faeces is ejected as pellets. Carbohydrates are generally absorbed as monosaccharides, so that disaccharides and polysaccharide are broken down into monosaccharide. For insect nutrition, the micronutrient required are sterols, vitamins and some minerals. The major dietary components are carbohydrates, lipids, proteins and nucleic acids. Insects with different larval stages also have the advantage of consuming different food sources by which the larvae avoiding competition with the adults, such as the hungry caterpillar who eats foliage, whereas the adult moth or butterfly may feed on nectar. Many microorganisms have capacity to consume nitrogenous waste of insects.

Fungi show mutualisms with numerous insects in Phylum Arthropoda: joint-legged invertebrates with a chitinous exoskeleton. They act as ectosymbiotic fungi. Arthropods depend on the fungus for the protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The fungal mycelium protects the insect colonies. Some bacteria supply nutrient to their host. *Riesiapediculicola* is a primary bacterial endosymbiont in body lice *Pediculus humanus*, and supplement their hosts with vitamin B, especially pantothenic acid.

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4.12 TERMINAL QUESTIONS AND ANSWERS

Question 1. Describe the food feeding mechanism in insects**.**

Question 2. Define ectosymbiostic fungi and endosymbiont with giving example.

Question 3. Give detail account on the modification of alimentary canal in insects.

Question 4. Explain nutrition and nutritional requirement in insects.

Question 5. Give the process of digestion in insects with suitable diagrams**.**

UNIT 5: CIRCULATORY SYSTEM

CONTENTS:

5.1 Objectives
5.2 Introduction
5.3 Circulation
5.4 Types of haemocytes
5.5 Haemopoetic organ
5.6 Changes in haemocyte number
5.7 Haemolymph protein
5.8 Summary
5.9 Terminal Questionsand Answers

5.1 OBJECTIVES

After studying this unit, the students will be able to pursue the knowledge about

i. Circulatory system in insects.
ii. Types of haemocytes and changes in its numbers.
iii. Haemopoetic organ and its functions.
iv. Haemolymph protein and its functions.

5.2 INTRODUCTION

In the previous chapter, digestive system has been discussed giving much emphasis on the food and nutrition in insects. In insects, open circulatory system is present, which is devoid of vessels so blood directly flow with into the body cavity. The nutrients, salts, hormones and metabolic wastes passes throughout the insect body with the help of circulatory system. The body cavity (haemocoel) is divided into three sinuses by diaphragm, a dorsal pericardial sinus, perivisceral sinus, and a ventral perineural sinus.

Diaphragm is formed by connective tissues and alary muscles. The function of alary muscles is to support the dorsal vessel. The dorsal vessel is divided into posteriorly heart and anteriorly aorta. The wall of dorsal vessel is contractile. It consists of spiral and circular muscle fibrils. Haemolymph is usually a clear colourless fluid, however, due to the presence of certain pigments, insects may be slightly green, yellow or red. Chemically, haemolymph composed of water, inorganic constituents, nitrogen wastes, organic acids, carbohydrates, lipids, amino acids, protein, pigments and gases. Haemolymph is unidirectionally circulated to appendages by various tubes, septa, valves and pumps. Circulation occurs in the wings of young adult. In wing circulation is sustained by influxes of air into the wing veins, rather than any pulsatile organs. Pulses of air in the fine tracheal tubes of the veins push the haemolymph through the enclosed space of the veins. Haemolymph contains a fluid portion called plasma and cellular fraction called haemocytes.

Blood cells or haemocytes are suspended in haemolymph are mesodermal and do not contain pigments. Types of haemocytes are prohaemocytes, plasmohaemocytes, coagulocytes, granular phagocytes, oenocytoids, spherule cells and adipohaemocytes. Haemolymph can function as hydraulic fluid, for example, in the expansion of newly molted butterfly wings and serve important role in immune system and in transport of hormones, nutrient and metabolite.Hemocytes proliferation takes place in specialized hematopoietic organs. Hematopoietic organs provide an environment where undifferentiated blood stem cells are able to self-renew, and at the same time generate offspring that differentiate into different blood cell types.

5.3CIRCULATION

Insects have open type blood circulatory system which is devoid of arteries and veins. So, the haemolymph freely flows throughout the body and transport nutrient, hormones and remove wastes. Dorsal vessel is the main structural component of an insect’s circulatory system. It is a simple tube-like structure composed of myocardial cell. This tube runs longitudinally through the thorax and abdomen. Anterior part of dorsal vessel called aorta and posterior part called heart. It is segmentally divided into chambers that are separated by valves (ostia) to ensure unidirectional or one-way flow of haemolymph. Alary muscles, which are present laterally at the wall of chamber show peristaltic contraction by which the haemolymph flow forward from one chamber to other. The heart contraction rate varies from one species to species from 30 to 200 beats per minute. During relaxation phase, the ostia open to permit the inflow of haemolymph from body cavity.

To facilitate the circulation of haemolymph the body cavity (haemocoel) is divided into three compartment-

1. Dorsal pericardial sinus
2. Perivisceral sinus
3. Perineural sinus

The sinuses are separated by septa or diaphragm. The dorsal diaphragm across the abdominal cavity and divided the haemocoel into pericardial sinus and visceral sinus. Ventral diaphragm forms continuous ventral sheath. It encloses the perineural sinus and extends from prothorax to the end of the body.

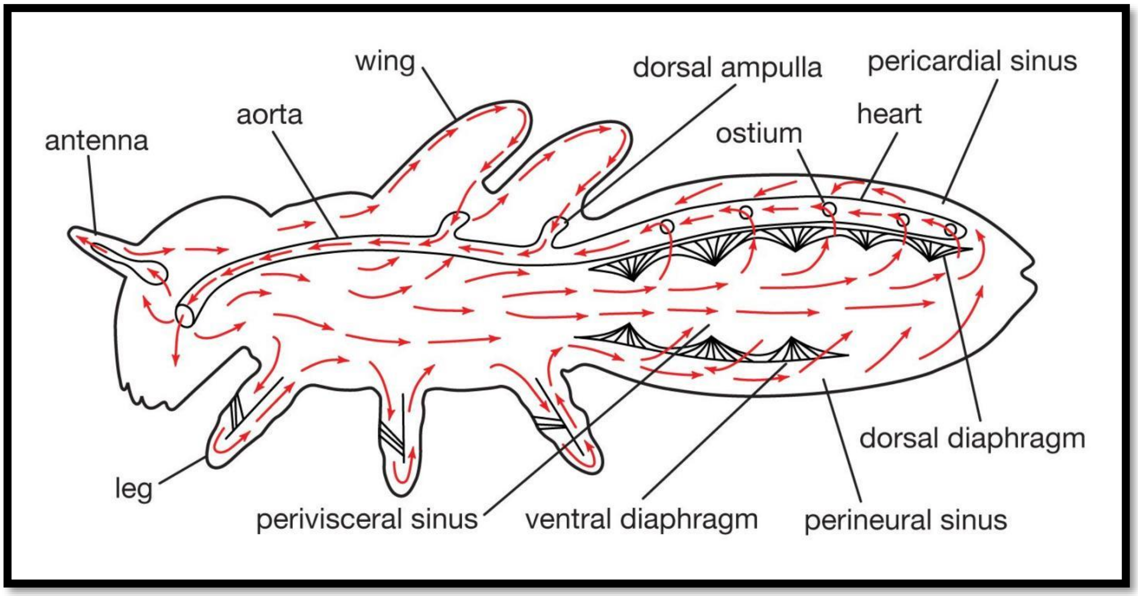

Fig. 5.3a: Circulatory system of Insect.

Insects have accessory pulsating organ that maintain the circulation through appendages. In most of adult insect, the pulsatile organ is present in wing bearing segment. It is also present at the base of antennae. It consists of ampulla from which a fine tube extends to the tip of antennae. Hemolymph is supplied to antennae and cerci by arteries connected to the dorsal vessel. In higher insects, however, these arteries were decoupled and associated with autonomous pumps that entered their body plan as evolutionary innovations. To ensure hemolymph supply to legs, wings, and some other appendages, completely new accessory pulsatile organs evolved. The muscular components of these pulsatile organs and their elastic antagonists were recruited from various organ systems and assembled to new functional units. In general, it seems that the evolution of accessory pulsatile organs has been determined by developmental and spatial constraints imposed by other organ systems rather than by changes in circulatory demands.Hemolymph is pumped throughout an insect’s body and appendages by wave-like contractions of the dorsal vessel, assisted by additional "hearts" or accessory pulsatile organs (APOs). Flow within the head, thorax, and abdomen is open (unconstrained to vessels) and pulsatile. In these regions, hemolymph is moved in bulk by pumping of the tube-like dorsal heart.

Wings are a key innovation in insects, enabling a myriad of ecologically important behaviors including predation, migration, and pollination. Although their composition of thin membranes and long tubular veins might superficially suggest otherwise, insect wings are dynamic, living structures that require a supply of vital substances. Veins provide mechanical integrity but also act as channels, containing tracheal tubes for gas exchange, nerves that provide sensory information in flight, and perhaps most importantly, hemolymph that serves multiple functions. Insect wings are living, flexible structures composed of tubular veins and thin wing membrane. Wing veins can contain hemolymph (insect blood), tracheae, and nerves. Continuous flow of hemolymph within insect wings ensures that sensory hairs, structural elements such as resilin, and other living tissue within the wings remain functional. It is well known that hemolymph circulates through insect wings. Over the last 100 years, scientists have developed experimental methods including microscopy, fluorescence, and thermography to observe flow in the wings. Recognizing and evaluating the importance of hemolymph movement in insect wings is critical in evaluating how the wings function both as flight appendages, as active sensors, and as thermoregulatory organs. They reviewed the history of circulation in wings, past and present experimental techniques for measuring hemolymph, and broad implications for the field of hemodynamics in insect wings.

Hemolymph actively circulates through wing veins and is critical for maintaining sensory structures that populate the wing. Movement of hemolymph, cells, and waste is also required for the proper development of the wing. At metamorphosis, movement of hemolymph in and out of the wing contributes to the expansion and unfolding of the wing. Unlike in the hemocoel, once it enters the wings, hemolymph is mostly constrained to a vessel network. Additionally, hemolymph flow may be affected by compression and reinflation of parts of the tracheal system, and possibly displacement of the gut system.

Insect wings exhibit two main hemolymph flow patterns: tidal (also known as ‘oscillatory’) and circuitous. In the 1980s, Lutz Wasserthal challenged the historical assumption that all flow was circuitous and discovered that lepidopterans employ tidal flow, and that tracheal expansion and compression influences wing hemodynamics. Generally, a tidal pattern involves hemolymph moving into all wing veins, and then reversing direction, coordinated by wing hearts, the dorsal vessel, thoracic air sacs, and wing tracheae. Quantitative measurements in Lepidoptera, Diptera, and Coleoptera suggested that tidal flows of hemolymph are possible with vigorous pumping of the wing hearts (pulling hemolymph from the wing), dorsal vessel reversals, coupling of wing tracheal tubes (expansion and compression), and inflation of thoracic air sacs. Large air sacs expand and compress between the hindwing and forewing hinges. In addition, visible through microscopy, sections of tracheal branches near the wing tip expand and contract, also affecting local flows.

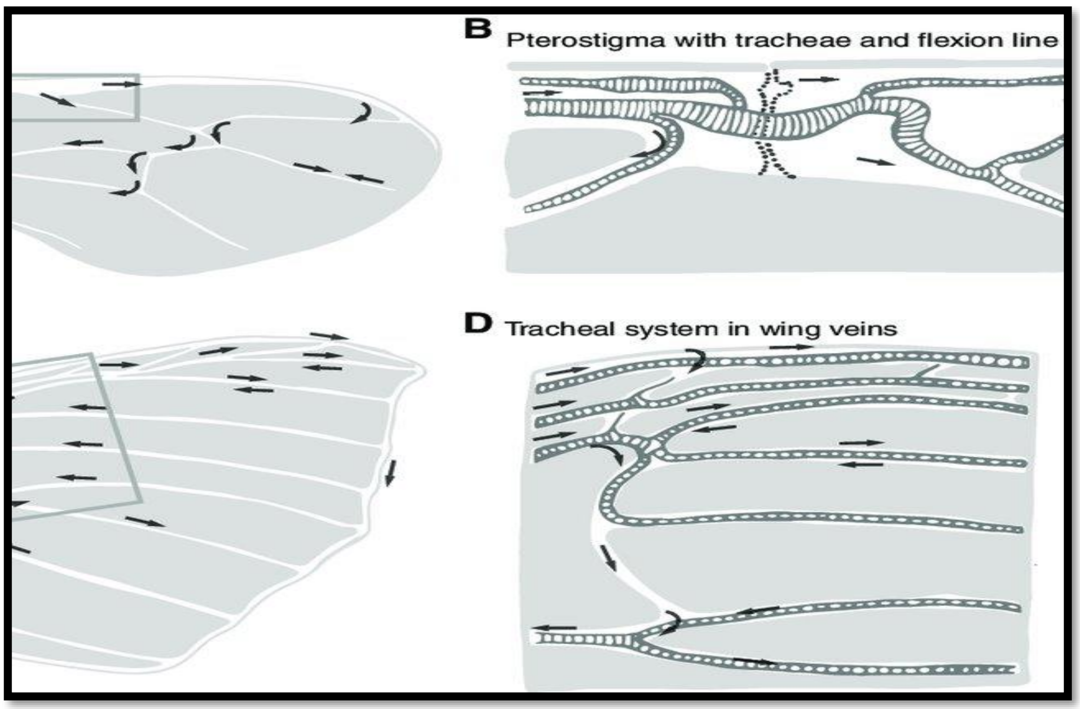

Fig.5.3b: Circulation pattern in insect wing.

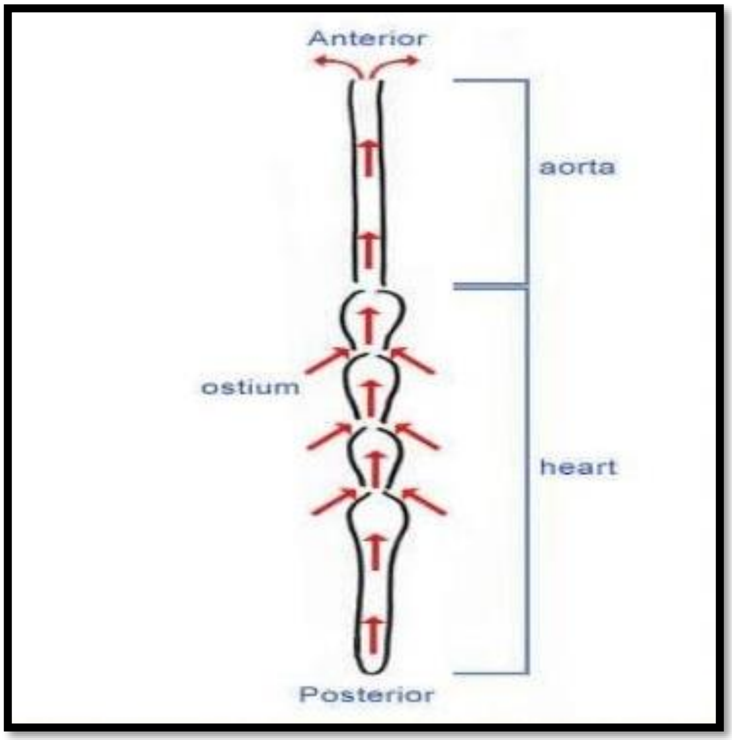

Fig.5.3c: Dorsal vessels and ostia of insect.

In most insects, the ampullae have dilator muscles whose function to pump haemolymph into the abdomen. A longitudinal septum is found in the legs of most insects. The septum divides lumen into sinuses and permit a bidirectional flow of blood within the leg. During systole, the blood is pumped forward through heart, entering the perivisceral sinus through anterior opening of aorta in the head and through excurrent ostia. The valves present in anterior opening prevents the escape of blood. Movement of ventral diaphragm help to maintain the supply of blood to ventral nerve cord. During diastole, blood is drawn into the heart through ostia.

The circulatory organs of the cricket ovipositor have a unique functional morphology. The pumping apparatus at the base of each ovipositor valve operates like a bellow. It forces hemolymph via sinuses delimited by thin septa of connective tissue in a countercurrent flow through the valve lumen. The pumping activity is based on neurogenic control by a central pattern generator in the terminal ganglion.

The coordination between circulation, respiration and abdominal movements were found in pupae of *Pieris brassicae, Tenebrio molitor, Galleria mellonella*and*Leptinotarsadecemlineata*. Coordination principles depend on metabolic rate: the need to support circulation with abdominal movements appears only at higher metabolic rates. Integration between different abdominal movements and circulation depends on species, on physiological state and, on internal morphology. At low metabolic rates, there is no need for a very intensive hemolymph flow, and the dorsal vessel is capable of initiating and/or maintaining necessary hemolymph flow. Starting from a certain metabolic level, it is possible that the abdomen is used to accelerate hemolymph flow in the case of a large amount of hemolymph. When the necessary flow speed has been reached, relatively weak pulsation of the dorsal vessel with accessory pulsatile organs and diaphragms can easily maintain the necessary flow intensity. Heart activity may sometimes be initiated by abdominal movements via cardiac reflex or mechanical excitation. Sometimes, when heart function is weakened by histolysis, the abdomen may temporarily take over the main circulatory function or occasionally contribute to acceleration of low-speed hemolymph flow. In this case the functions are simultaneous and may be triggered by some mediator(s). In active adult insects the whole body is moving, and hence hemolymph circulates and the tracheal system is effectively ventilated by a whole-body ensemble consisting of the dorsal vessel, moving organs, body appendages and accessory pulsatile organs. However, the functional compartmentalization in the hemocoel of insects may provide an explanation for how fluid flows are managed in an open circulatory system. Narrow-waisted insect create sustained pressure differences across segments, but their constricted waist provides an evident mechanism for compartmentalization. Insects with no obvious constrictions between segments may be capable of functionally compartmentalizing the body, which could explain complex hemolymph flows. Here, they test the hypothesis of functional compartmentalization by measuring pressures in a beetle and recording abdominal movements. The pressure is indeed uniform within the abdomen and thorax, congruent with the predicted behavior of an open system. However, during some abdominal movements, pressures were on average 62% higher in the abdomen than in the thorax, suggesting that functional compartmentalization creates a gradient within the hemocoel. Analysis of volume change suggests that the gut may play an important role in regulating pressure by translating between body segments.

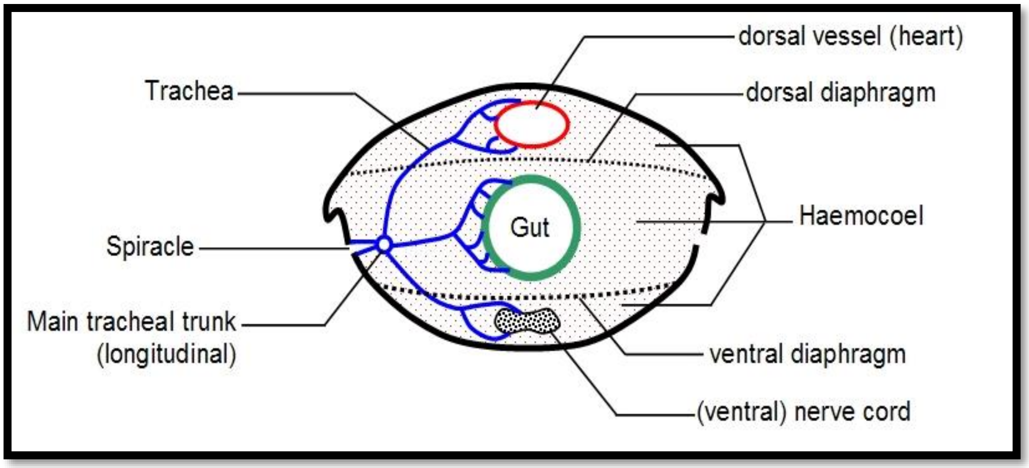

Fig. 5.3b: Transverse section of insect abdomen.

Hemolymph is driven through the antennae of *Drosophila melanogaster* by the rhythmic contraction of muscle, which runs through the brain. Contraction results in the expansion of an elastic ampulla, opening ostia and filling the ampulla. Relaxation of the ampullary membrane forces hemolymph through vessels into the antennae. The activity of muscle contraction leads to the rapid perfusion of the antenna by hemolymph. In addition, it leads to the rhythmic agitation of the brain, which could be important for clearing the interstitial space.

Studies on the physiology of insect circulation have revealed that the insect central nervous system can exert a strong nervous control over certain dorsal vessels and diaphragms. The central nervous and skeletal neuromuscular systems, not one neurotransmitter substance has been identified in any of the vessels, pumps or diaphragms responsible for circulation in insects. The circulatory systems of cockroach, locust, fly, moth and bee all involve unique specializations. It is suggested that an autonomic nervous system is present in insects and is responsible for coordination and control of both circulation and respiration.

5.4TYPES OF HAEMOCYTES

Haemocytes or blood cells are suspended in haemolymph. Haemocytes are mesodermal in origin. Nutrients, nitrogenous waste products, hormones, and a variety of other substances also are transported in the hemolymph for distribution to various tissues. In most insect larvae, the hemocytes are produced within hematopoietic organs (blood cell producing factories) where they replicate and differentiate. The number and types of hemocytes vary with insect species, developmental stage, and physiological state.

A number of morphological distinct cells have been identified in the haemolymph such as-

1) Prohaemocytes – These are small rounded cells with relatively large nuclei and basophilic cytoplasm, also give rise other haemocytes so called stem cell.

2) Plasmohaemocytes- These are most abundant, variable in form, phagocytic with basophilic cytoplasm. They have spherical nucleus in center which is surrounded by vacuolated cytoplasm. Plasmocytes contain Golgi apparatus and endoplasmic reticulum. Besides these, lysosome are also present in them. They show amoeboid movement and phagocytosis. They are responsible for cellular immunity of insects, as they encapsulated the foreign agent by phagocytic action

3) Coagulocytes- These are granular cells having small nucleus and pale and hyaline cytoplasm containing black granules.

4) Granulocytes- These are phagocytic with acidophilic granules in cytoplasm. They have round nucleus surrounded by cytoplasm and also have well developed granular rough endoplasmic reticulum and Golgi apparatus. They are obtained from plasmatocytes. They show defensive mechanism by discharging their contents on surface of organism.

5) Oenocytoids- Usually large, thick, basophilic cytoplasm having canaliculi.These types of cells are mainly found in Lepidoptera. They show little developed Golgi complex, rough endoplasmic reticulum and have complex microtubules.

6) Spherulocytes - These are round, oval and filled with large, non-refringent, usually acidophilic inclusions.

7) Adipophaemocytes- These are spheroidocytes having refringent fat droplets. They have well developed Golgi body and endoplasmic reticulum.

Number of hemocytes and whether or not they circulate can depend on development stage and potential stress events (e.g., wounding, infection). For example, in adult mosquitoes, there may be 500-4000 circulating hemocytes, while in other dipteran, lepidopteran, and orthopteran insects, cell densities range from 500-900 hemocytes per microlitre . Hemocytes can range in size depending on species and if the cell is "active." The mosquito hosts three types of hemocytes granulocytes (9 µm diameter but can spread to 35 µm diameters when attached to foreign surfaces), oenocytoids (9 µm diameter), and prohemocytes (4-6 µm diameter). In smaller insects, some appendages, such as wings, are too small to allow for cells to enter the wings, but hemolymph continues to circulate. For example, in mosquitoes, flowable space within the wing circuit is only 1 µm in diameter, whereas circulating hemocytes are typically 8 µm or larger in Diptera. Smaller organisms, such as *Plasmodium* sporozoites, bacteria, and other viruses have been found in mosquito wings, suggesting that active circulation is important for dissemination of immune factors.

In insects with vein diameters large enough to accommodatecells,hemocytes can be visualized and used to identify flow direction. In fact, entomologists first recognized hemolymph in insects by tracking visible circulating hemocytes within larger insects. Recently observed in Nymphalid butterflies, hemocytes clearly circulate in veins and through major organs such as scent patches. It is not known how hemolymph velocities and hemocyte circulation scale within insect wings of increasing size, nor how hemolymph movement changes with development and age. Flow metrics such as velocity, acceleration, and heart pumping frequency have been quantified for adult mosquitoes (*Anopheles gambiae*) and North American grasshoppers (*Schistocerca americana*).

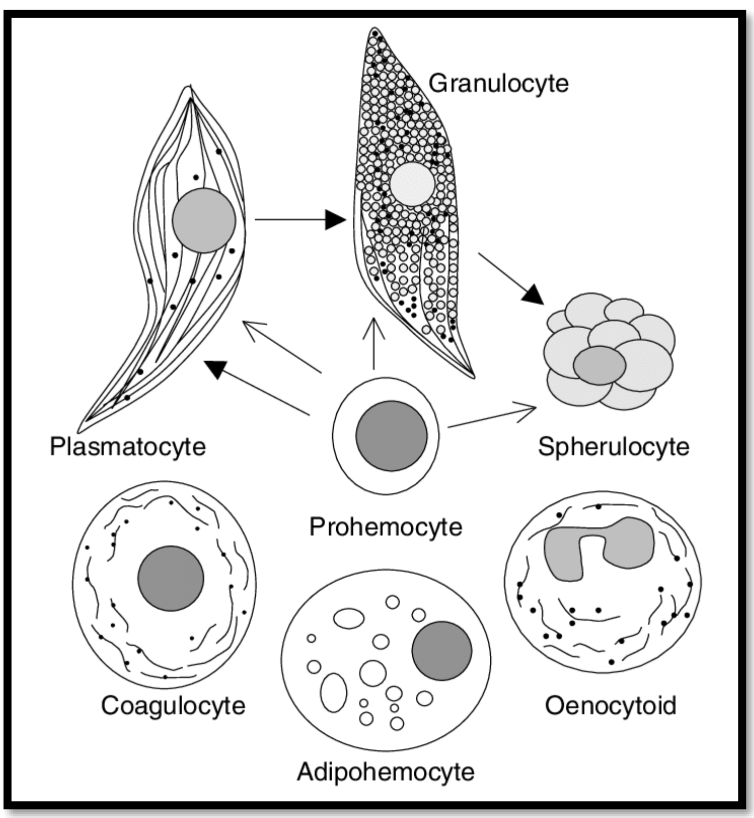

Fig. 5.4a: Types of haemocytes in insect.

Function of haemocytes-

1) Phagocytosis- Plasmatocytes and granulocytes ingest foreign particles, bacteria and cellular debris. They are also important during period of moulting and metamorphosis, when the histolysis takes place. They also defense against disease and remove dead and decaying cells.

2) Nodule formation- Nodule formation occurs in response of higher number of bacteria and protozoan invasions. Nodules are aggregates of entrapped foreign materials surrounded by plasmatocytes.

3) Encapsulation- When foreign organismsare too large for either phagocytosis or nodule formation, they are destroyed by encapsulation. In this process, foreign body is randomly contacted by granulocytes which recognizes the foreign body. The granulocytes degranulates and the material sticks to the foreign body, which is followed by the additional granulocytes attacking to foreign body. Plasmatocytes, then flattened and spread over the foreign body surface increasing the number of layers around the foreign body until it is longer recognized as foreign. As a result of asphyxiation and starvation, the encapsulated organism dies.

4) Wound healing- Several haemocytes (plasmocytes and spherule cells) tend to accumulate at the sites of injury, where they may be phagocytic, promote coagulation by granulocytes and form protective sheets for helping in healing.

5) Haemostasis, coagulation and plasma precipitation- Haemocytes prevents loss of haemolymph at a wound site by plugging and promoting coagulation or plasma precipitation. In cockroaches, a clump of hemocytes are formed; the blood cells become round, develop thread – like pseudopodia, and agglutinate to form a plug, which is the essential factor of the clot. When blood cells coagulate due to the presence of hyaline hemocytes, these cells extrude thread – like pseudopodial expansions, which fuse to form a meshwork in which the other cells are entangled.

6) Protection- The insect immune system refers to mechanisms that permit the insect to resist infection by microorganisms. The humeral immune factors found in the haemolymph consists of two basic type: non inducible and inducible. Inducible factors in haemolymph include antibacterial proteins and lysozyme, whereas non inducible factor are lectins produce a cascade of chemical events that ultimately kill the invader.

7) Secretion and formation of other tissues- Haemocytes are involved in the formation of the basement membrane underlying the epidermal cells and possibly the sheath material surrounding the muscles. In some insects, haemocytes were observed to activate the prothoracic glands before moulting, some haemocytes may also be involved in the formation of the fat body. Haemocytes also be involved in the detoxification, lubricant, hydraulic medium and heat transfer.

5.5HAEMOPOETIC ORGANS

In vertebrates and insects, common progenitors, called hemangioblasts, give rise to the endothelia and blood cells. In the adult animal, many differentiated hemocytes seem to retain the ability to proliferate; however, in most cases investigated closely, the bulk of hemocyte proliferation takes place in specialized hematopoietic organs. Hematopoietic organs provide an environment where undifferentiated blood stem cells are able to self-renew, and at the same time generate offspring that differentiate into different blood cell types.

Hemocytes replicate within hematopoietic organs, as circulating cells, and as sessile cells. Insects fight infection by Immune responses that are mediated by hemocytes, the fat body, the midgut, the salivary glands and other tissues. Immune system recognized foreign organisms that have entered the body of an insect when pathogen-associated molecular patterns bind host-derived pattern recognition receptors. This, in turn, activates immune signaling pathways Toll, Imd, Jak/Stat, JNK, and insulin that amplify the immune response, induce the production of factors with antimicrobial activity, and activate effector pathways. By the Activation of these and other pathways leads to kill pathogen through various process that is phagocytosis, melanization, cellular encapsulation, nodulation, lysis, RNAi-mediated virus destruction, autophagy and apoptosis. Protects entire groups.

Hematopoiesis is well-conserved between *Drosophila* and vertebrates. Similar as in vertebrates, the sites of hematopoiesis shift during *Drosophila* development. Blood cells (hemocytes) originate *de novo* during hematopoietic waves in the embryo and in the *Drosophila* lymph gland. In contrast, the hematopoietic wave in the larva is based on the colonization of resident hematopoietic sites by differentiated hemocytes that arise in the embryo, much like in vertebrates the colonization of peripheral tissues by primitive macrophages of the yolk sac, or the seeding of fetal liver, spleen and bone marrow by hematopoietic stem and progenitor cells. At the transition to the larval stage, *Drosophila* embryonic hemocytes retreat to hematopoietic "niches," i.e., segmentally repeated hematopoietic pockets of the larval body wall that are jointly shared with sensory neurons and other cells of the peripheral nervous system (PNS). Hemocytes rely on the PNS for their localization and survival, and are induced to proliferate in these microenvironments, expanding to form the larval hematopoietic system. In this process, differentiated hemocytes from the embryo resume proliferation and self-renew, omitting the need for an undifferentiated prohemocyte progenitor.

Drosophila melanogaster and comparing to data from other drosophilids, the malaria mosquito, *Anopheles gambiae*, and the silkworm, *Bombyx mori*. Basically, the new data support the presence of a few major classes of hemocytes:

(1) A highly heterogenous and plastic class of professional phagocytes with many functions, called plasmatocytes in *Drosophila* and granular cells in other insects.

(2) A conserved class of cells that control melanin deposition around parasites and wounds, called crystal cells in *D. melanogaster*, and oenocytoids in other insects.

(3) A new class of cells, the primocytes, so far only identified in *D. melanogaster*. They are related to cells of the so-called posterior signaling center of the larval hematopoietic organ, which controls the hematopoiesis of other hemocytes.

(4) Different kinds of specialized cells, like the lamellocytes in *D. melanogaster*, for the encapsulation of parasites. These cells undergo rapid evolution, and the homology relationships between such cells in different insects are uncertain.

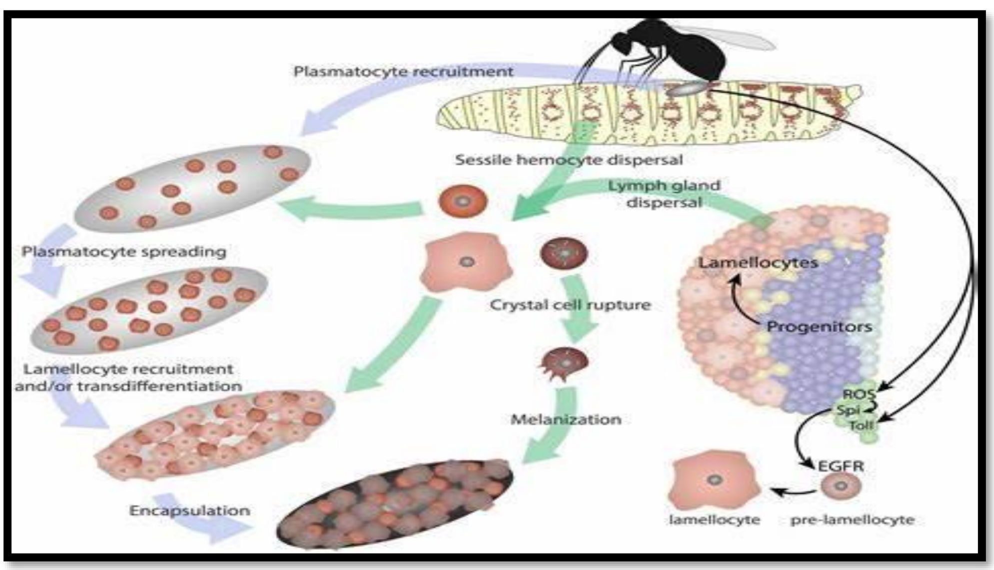

Fig. 5.5a: Drosophila as a genetic model of haematopoesis.

5.6 CHANGES IN HAEMOCYTE NUMBER

All the haemocytes develop from mesodermal prohaemocytes in haemocytopoetic organs. The total number of haemocytes per unit volume varies from 10-1, 67000µl. Certain Diptera larva have no haemocytes in circulation. The number of haemocytes tends to increase during larval instars, decline in the pupal stage, and increase initially and then decline in adult stage. Plasmatocytes and granulocytes are most abundant.

The changes in total haemocyte counts (THC) in relation to sex, development, ecdysis, and hot-water fixation in *Halys dentata* (Hemiptera). Whereas, statistically there is no difference in the THC of the two sexes, the THC differs in the immature stages and adults. There is a gradual increase in counts during metamorphosis. The fixation of insects in hot water before withdrawal of haemolymph sharply affects the THC and it shows a significant increase in the number of haemocytes. Studies made in relation to ecdysis show that the THC slightly decreases 24 hr. before ecdysis, whereas after ecdysis it sharply falls and then rises again during the middle part of the instar.

Twenty-four hoursafter wounding, there was a significant increase in the number of circulating haemocytes/mm^3 in wounded as compared to unwounded insects. This increase was accompanied by increases in round plasmatocytes, granular haemocytes, prohaemocytes, and spherule cells and a decrease in the adipohaemocytes. During initial stage of wound healing, the mitotic activity of haemocytes was greatly increased.

Winter period is energetically challenging for temperate insects, as food resources are very limited and great majority of species are not feeding at all in the course of overwintering. The physiological and immunological parameters in laboratory-reared and field-collected harlequin ladybirds (*Harmonia axyridis*). For laboratory-reared beetles, they focused on the effects of winter temperature regime (cold, average, or warm winter) on total haemocyte concentration aiming to investigate potential effects of ongoing climate change on immune system in overwintering insects. The strong reduction in haemocyte concentration during winter; however, there were only limited effects of winter temperature regime on changes in haemocyte concentration in the course of overwintering. For field-collected beetles, they measured additional parameters, specifically: total protein concentration, antimicrobial activity against Escherichia coli, and haemocyte concentration before and after overwintering.

The total haemocyte count and haemolymph volume in *Periplaneta americana* (L.) with special reference to the last moulting cycle. The calculated number of haemocytes in the entire insect gives far more reliable information concerning changes in haemocyte numbers than total haemocyte counts (THC) alone because the latter obviously will vary according to the haemolymph volume. The absolute number of circulating haemocytes in the entire *Periplaneta americana* (L.) does not increase prior to ecdysis even though the number of haemocytes per cubic millimetre increases. This relative increase in haemocytes is due to a decrease in haemolymph volume. The absolute number of circulating haemocytes does not decline at ecdysis itself even though there is a significant decrease in the number of haemocytes per cubic millimetre. This relative decrease in THC is directly related to a significant increase in the haemolymph volume. At ecdysis there is a great increase in coagulability of the haemolymph and in absolute numbers of one specific type—the cystocytes (= coagulocytes). However, the absolute number of circulating haemocytes significantly decreases 24 hours after ecdysis, but there is no change in the number of haemocytes per cubic millimetre at this time because the haemolymph volume has returned (decreased) to normal. Simultaneously, there is a significant decrease in the absolute numbers of circulating cystocytes and a decrease in the coagulability of the haemolymph.

The changes in haemocyte morphology and differences in haemocyte counts during the immune response of *Culex quinquefasciatus* (Diptera: Culicidae) to microfilariae of *Wuchereriabancrofti.* The mean number of total haemocytes was significantly elevated in infected mosquitoes ($P<0.001$), reaching a peak on the third day post-infection. Differential counts show that mean numbers of prohaemocytes, plasmatocytes, granular cells and oenocytoids increased significantly after infection with microfilariae granulocytes compared to the control group. Changes in proportional counts of haemocytes were also analysed in haemolymph perfusates of Culex quinquefasciatus infected with W. bancrofti. On the first day post-infection, infected mosquitoes showed an increase in the proportion of prohaemocytes (18.8% compared to 9.6% for the control) and of oenocytoids (7.1% compared to 4.7% control); however, they exhibited lower levels of plasmatocytes (36.6% compared to 42.1% control) and granular cells (36.1% compared to 41.4% control). On day 14 post-infection, similar changes were observed for these haemocyte types, except that the proportion of granular cells was significantly greater than the control (41.2% compared to 31.3% control). Although an enhancement of prohaemocyte numbers was observed, this cellular type did not show any ultrastructural alteration. On the other hand, granular cells, plasmatocytes and oenocytoids presented morphological alterations indicative of innate immunological activation in mosquitoes infected with W. *bancrofti*.

5.7 HAEMOLYMPH PROTEIN

In insects, the haemolymph contains several proteins. Proteins have different functions. Haemolymph is usually a clear colourless fluid, however due to the presence of certain pigments in few insects, it may be green, yellow and red. Certain midges (*Chiromonas* larva), backswimmers and the horse botfly contain haemoglobin. It makes up about 5-40 % of the total body weight of an insect.

Proteins present in haemolymph are:

Vitellogenin-The eggs from oviparous organisms contain large amounts of vitellus, or yolk, which are utilized by the growing embryoes. Vitellogenesis is the process of vitellus accumulation and involves massive heterosynthetic synthesis of the protein vitellogenin (Vg) and its deposition in the oocyte. Insectvitellogins (Vgs) are large molecules (~200-kD) synthesized in the fat body in a process that involves substantial structural modifications (e.g., glycosylation, lipidation, phosphorylation, and proteolytic cleavage, etc.) of the nascent protein prior to its secretion and transport to the ovaries. However, the extent to which Vitellogenin are processed in the fat body varies greatly among different insect groups. They provide evidence by cloning and peptide mapping of four Vg molecules from two cockroach species (*Periplaneta americana* and *Leucophaeamaderae*) that, in hemimetabolous insects, the pro-Vg is cleaved into several polypeptides (ranging from 50-to 180-kD), unlike the holometabolans where the Vg precursor is cleaved into two polypeptides (one large and one small). An exception is the Vg of Apocrita (higher Hymenoptera) where the Vg gene product remains uncleaved. The yolk proteins (YPs) of higher Diptera (such as *Drosophila*) form a different family of proteins and are also not cleaved. So far, Vgs have been sequenced from 25 insect species; 9 of them belong to Hemimetabola and 16 to Holometabola.

The hemolymph protein, mostly studied in ticks, has been vitellogenin (Vg). Vg is synthesized by the tick fat body after female adults obtain a blood meal, is released into the hemolymph and is absorbed by developing American dog tick, *Dermacentorvariabilis*, Vg is comprised of two native proteins and seven subunits on SDS-PAGE. Vg has been characterized in oocytes as vitellin (Vn).In general, the carbohydrates, lipids and amino acids composition is similar to insects except that in the tick, Vg contains heme, most likely from the digestion of host hemoglobin. Another predominant hemolymph protein, apparently a carrier protein (CP), has recently been studied in two tick species. This protein is found in the hemolymph of both male and female adults, in adult tissues outside of the hemolymph in some tick species, in coxal fluid of soft ticks and in whole body homogenates from eggs, larvae and nymphs. CP from the hard tick, *D. variabilis*, contains cholesterol, phospholipids, monoacylglycerides, triacylglycerides, free fatty acids, carbohydrates and heme. Carrier protein in the American dog tick consists of two subunits, one of which has 61% identity to the biliprotein, artemocyanin, from the fairy shrimp. CP is identical to a heme-lipoprotein (HeLp) from *Boophilusmicroplus*. The exact roles of CP and HeLp have not yet been fully determined, but they apparently are important in heme sequestration and as a storage depot for protein and lipids.

Storage proteins- Storage proteins present in haemolymph from larvae of Colarado potato beetle. Diapause protein 1, which occur in haemolymph of last instar larvae short day adults; appeared to be a storage protein. Diapause protein is composed of 82000 subunits. This protein dissociated into two bands due to high pH used non denaturing gel.

In many insects, storage proteins (SP) provide an amino acid reserve that can be used during metamorphosis and reproduction. In the lubber grasshopper, *Romaleamicroptera*, there are three abundant hemolymph proteins (~500kDa, ~200kDa, and ~90kDa) that rise and then decline during the oviposition cycle. They function as storage proteins to support oocyte development. To test the hypothesis that these proteins are related to other insect storage proteins, each protein was purified and their trypsin fragments sequenced by LC-MS (Liquid chromatography-Mass spectrometry). The amino acid sequences of these fragments were used to design degenerate primers, which were then used to amplify a cDNA fragment for each protein. The deduced amino acid sequences of thethree proteins are similar. Thus, the 90kDa protein is 46% and 38% similar to the 200kDa and 500 kDa proteins, respectively. The deduced sequences are also similar to many insect hexamerin storage proteins. For example, the 500kDa protein has 40% identity to the hexamerin precursor of *Blaberusdiscoidalis*, 32% identity to the juvenile hormone binding protein (JHBP) of *Locustamigratoria*, and 32% identity to the arylphorin-like hexamerin of *Aprionagermari*. Analogous to other insect hexamerin storage proteins, the mRNAs for these three proteins are also detected in the lubber fat body by Northern blot analysis.

Chromoprotein- The isolation and characterization of chromoprotein from larval haemolymph of Japanese oak silkworm (*AntheraeaYamamai*) by using four steps of chromatography: (a) hydrophobic interaction chromatography; (b) ion exchange chromatography; (c) gel-filtration; and (d) reverse-phase high performance liquid chromatography (HPLC). The two-protein designated as P-I and P-II. These two proteins were separated by TSKgel Phenyl-5PW RP column chromatography. P-I has an apparent molecular weight of 31,000 or 35,000, as determined by gel-filtration and SDS-PAGE, respectively. P-II shows a molecular weight of 22,000 or 25,000, by gel-filtration and SDS-PAGE, respectively. The molecular weight of P-I and P-II were determined to be 31,076 and 21,500 by MALDI-TOF MS, respectively. These results suggest that both P-I and P-II are monomers. The N-terminal sequence analysis suggests that P-I is closely related to the ommochrome-binding protein (OBP) from the hemolymph of *Manduca sexta*, with 40% identity in the first 30 residues, while P-II is similar to the biliproteins (BPs) from other lepidopteran insects (50% identity).

The two blue-pigment binding proteins, BP1 and BP2, are present in larval and pupal haemolymph of cabbage white butterfly, *Pieris rapae*, and vary in expression during development. Both BP1 and BP2 are found in pupal and adult haemolymph in varying proportions, while only small amounts of BP2 are found in larval haemolymph. BPs are separated by 75% ammonium sulfate, and then purified effectively by ion exchange column chromatography and preparative gel electrophoresis. It was shown that BP1 and BP2 have molecular masses of 20,244 and 19,878 Da, and isoelectric points of 7.0 and 6.8, respectively. Considering their amino acid compositions and N-terminal amino acid sequences, the two proteins are almost identical except the first N-terminal amino acid. The first amino acid of BP1 is asparagine, whereas the initial residue of BP2 is aspartic acid. Anti-BP1 cross-reacts with BP2, indicating that they have immunological homogeneity. Western blotting analyses revealed that only BP1 was present in the larval tissues such as fat body, integument, muscle, and hindgut. However, BP1 was not found in midgut, Malpighian tubules, and silk gland. BP1 was also present in the protein bodies, and both cuticle and hemocoel sides of larval epidermis cells by the transmission electron microscopic observation.

Lipid transport protein- Lipid transport protein (lipophorin) is present in haemolymph of insect whose main function is to transport cholesterol, diacylglycerol and hydrocarbon between tissues. lipophorin, formerly called the "diacylglycerol-carrying lipoprotein," exists in the hemolymph of many insects including locust, cockroach, and silkworm. A rapid and efficient method has been developed for the purification of lipophorin, which includes a specific precipitation under low ionic concentration and DEAE-cellulose column chromatography. The final preparation of lipophorin is highly homogeneous, as judged by gel electrophoresis, electron microscopy, and immunodiffusion. Molecules of lipophorin from the above three insects are almost globular in shape with a diameter of 13-16 nm. Molecular weights are 600,000-700,000, and the lipid content totals 40-50%. The lipids are comprised of diacylglycerol, cholesterol, and phospholipid. The locust and cockroach lipophorin contain large amounts of hydrocarbons in addition to the above lipids. Apoprotein of lipophorin consists of two-non-identical subunits, heavy chain (M.W. 250,000) and light chain (M.W. 85,000); carbohydrate (mainly mannose) is covalently associated only with the heavy chain. Insect lipophorin has multiple roles as a true carrier and a reusable shuttle in transporting diacylglycerol, cholesterol, and hydrocarbon from sites of storage, absorption, and synthesis to sites where these lipids are utilized as metabolic fuel, precursors of triacylglycerol and phospholipid synthesis, or structural components of cell membrane and cuticle.

Many insect species are almost completely dependent on lipids for their metabolic needs, although this is usually a function of developmental stage. The primary storage organ is the fat body, which can constitute 50% of the fresh weight of the insect and also acts as the major metabolic center. The main functions of which are to transport nutrient substrates to utilization sites and to deliver metabolic wastes to the excretory system.Although neutral lipids are stored as triglycerides, in times of need they appear to be endergonically released into the hemolymph as diglycerides in the majority of insects thus far studied (particularly silkmoths and locusts). Indeed, diglycerides constitute the largest neutral lipid fraction in the hemolymph of silkmoths, locusts, cockroaches, bugs, etc. In the hemolymph the diglyceride is found as a constituent of specific lipoproteins, and one specific lipoprotein class (lipoprotein I; high density lipoprotein) appears to be necessary for the transport of diglyceride from the fat body cell into the hemolymph. This particular lipoprotein is also involved in the transport of cholesterol from the gut into the hemolymph. Thus, lipoprotein I appears to be the major neutral lipid and sterol transport agent in the insects studied and, in addition, plays a regulatory role in the release of both diglycerides and sterols. Hemolymph lipoprotein II (very high-density lipoprotein) may be important in providing protein and lipid to the insect ovary during oogenesis. The insect growth hormone, juvenile hormone, is transported by hemolymph lipoproteins in silk moths and locusts.

Enzymes – Trehalose, esterase, lysozyme and phenol oxidases, and chitinase enzymes are found in haemolymph of insect. Alteration of enzymes in haemolymph of the silkworm, *Bombyx mori* during Grasserieinfection. A significant decrease in enzyme activity of alkaline phosphatase, acid phosphatase, alanine amino transferase, aspartate amino transferase, in the infected larvae as compared with control healthy silkworms.The haemolymph of the active fourth instar larva of the pink bollworm, *Pectinophoragossypiella* contains lactic dehydrogenase (L.D.H.), alkaline phosphatase, glutamic oxaloacetic transaminase (G.O.T.) and glutamic pyruvic transaminase (G.P.T.). The activities of L.D.H., alkaline phosphatase and G.P.T. declined in the haemolymph of diapausing larva at various degrees. During diapause termination the activities of these three enzymes increased at first and then decreased later on. G.O.T. increased in activity in the haemolymph of diapausing larva and decreased successively thereafter during diapause termination.

Immune response protein- Lipophorin also help in insect defense system. The protein moiety of lipophorin comprises two glycosylated apolipoproteins, apolipophorin I (apoLp-I) and apolipophorin II (apoLp-II), constantly present in a lipophorin particle, and an exchangeable protein, apolipophorin III (apoLp-III). ApoLp-III is an abundant protein occurring in hemolymph in lipid-free and lipid-bound state and playing an important role in lipid transport and insect innate immunity. In immune response apoLp-III serves as a pattern recognition molecule. It binds and detoxifies microbial cell wall components, i.e. lipopolysaccharide, lipoteichoic acid, and beta-1, 3-glucan. ApoLp-III activates expression of antimicrobial peptides and proteins, stimulates their antimicrobial activity, and participates in regulation of the phenol oxidase system and in hemolymph clotting. In addition, the protein is involved in cellular immune response, influencing hemocyte adhesion, phagocytosis and nodule formation, and in gut immunity.

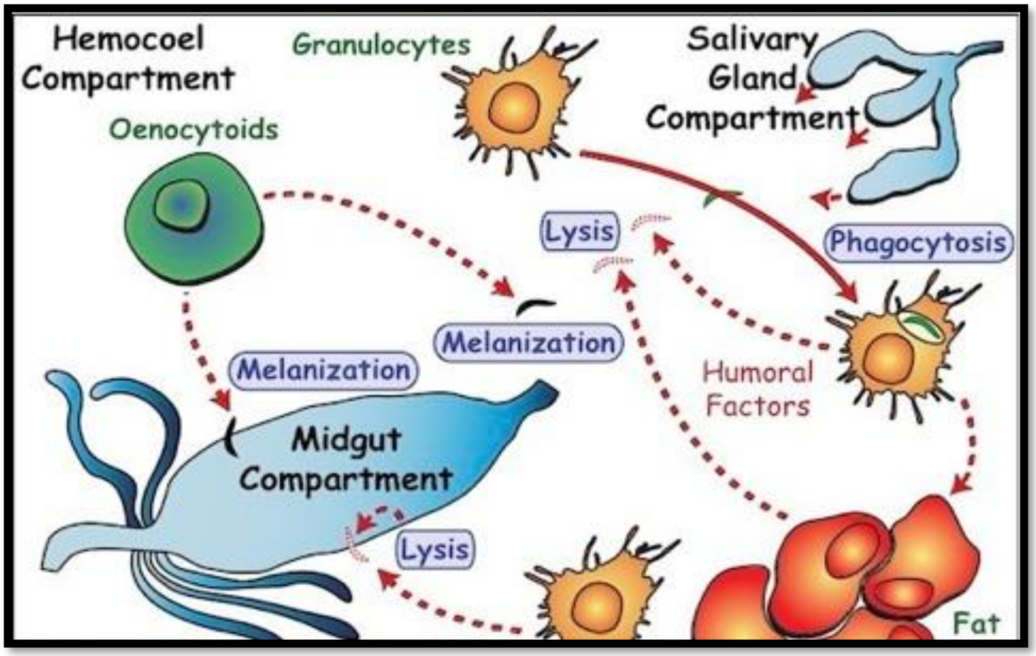

Fig. 5.7a: Mosquito innate immunity.

Mosquito lives under risk of infection. As adult mosquitoes acquire pathogens through blood feeding, sugar feeding, injury induced breaks the cuticle and pathogen- driven cuticular degradation. Mosquito kill pathogen through three mechanism: cell mediated phagocytosis, melanization and lysis. All can be initiated by pathogen recognition factor and the factor leading to killing can be subdivided into cellular and humoral components. The cellular responses include phagocytosis, encapsulation by haemocytes and pericardial cells. The humoral response includes Phenol oxidase cascade system of melanization and wound healing, inducible antimicrobial peptides, reactive oxygen and nitrogen intermediates and pattern recognition receptors.

Hemocyte-mediated immune response found in mosquito haemocoel. The cellular immune responses found in three different mosquito genera (*Anopheles gambiae, Aedes agepti*and*Armigeressubalbatus*).

Proteinase inhibitor- Proteolytic signaling cascades control a wide range of physiological responses. In order to respond rapidly, protease activity must be maintained at a basal level: the component zymogens must be sequentially activated and actively degraded. The insects have a wide range of trapping- and tight-binding protease inhibitors, which can regulate the activity of individual proteases. In addition, the interactions between component proteases of a signaling cascade can be modified by serine protease homologues. The tight-binding inhibitors have a lock-and-key mechanism capable of high target specificity. In addition, proteins containing multiple tight-binding inhibitory domains may act as scaffolds for the assembly of signaling complexes. Proteolytic cascades regulated by combinations of different types of inhibitor could combine the rapidity of suicide-inhibitors with the specificity lock-and-key inhibitors.

Serpins, a protease inhibitor perform various physiological functions in insects, including development, digestion, host-pathogen interactions, and innate immune response. In insects, the innate immune system is characterized as the first and major defense system against the invasion of microorganisms. Serine protease cascades play a critical role in the initiation of innate immune responses, such as melanization and the production of antimicrobial peptides, and are strictly and precisely regulated by serpins.

5.8 SUMMARY

Insect circulatory system involved in a vital physiological process. The open blood circulatory system is found in insect. The circulatory system helps in transport of nutrient, hormone and metabolic wastes. Dorsal vessel is a simple tube-like structure run longitudinally through thorax and abdomen. Its anterior part is called aorta and posterior part is called heart. The flow is unidirectional. The peristaltic contraction of alary muscles flow haemolymph from one chamber to the other. The circulation is carried in three compartments, viz. dorsal pericardial sinus, perivisceral sinus and perineural sinus. The sinuses are separated by septa or diaphragm. Beside this, insects have accessory pulsatory organ which is also present at the base of antennae. The presence of valves prevents escape of blood.

Haemocytes are present in haemolymph which are mesodermal in origin. These are produced within haemopoetic organ. The number and types of hemocytes vary with insect species, developmental stage, and physiological state. The types of haemocytes areprohaemocytesplasmohaemocytes, coagulocyte, and granulocyte, Oenocytoids, Spherulocytes and Adipophaemocytes. The plasmohaemocytes and granulocytes ingest foreign particles, bacteria and cellular debris by the process of phagocytosis. They also defense against disease and remove dead and decaying cell. When foreign organisms are too large for either phagocytosis or nodule formation, they are destroyed by encapsulation Several haemocytes (plasmocytes and spherule cells) tend to accumulate at the sites of injury where they may be phagocytic, promote coagulation by granulocytes and form protective sheets for helping in healing.

Haemocytes prevent loss of haemolymph at a wound site by plugging and promoting coagulation or plasma precipitation. The insect immune system refers to mechanisms that permit the insect to resist infection by microorganisms. Hemocytes replicate within hematopoietic organs, as circulating cells, and as sessile cells. Insects fight infection by Immune responses that are mediated by hemocytes, the fat body, the midgut, the salivary glands and other tissues. Immune system recognized foreign organisms that have entered the body of an insect when pathogen-associated molecular patterns bind host-derived pattern recognition receptors. Haemocytes are involved in the formation of the basement membrane.

Haemocytes role in the detoxification, lubricant, hydraulic medium and heat transfer. The total number of haemocytes per unit volume varies from 10-1, 67000µl.Plasmatocytes and granulocytes are most abundant. Protein present in haemolymph are Vitellogin, storage protein, chromoprotein, lipid transport protein, enzymes, proteinase inhibitor and immune response protein.

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5.9TERMINAL QUESTIONS AND ANSWERS

Question 1. Write the composition and main function of haemolymph.

Question 2. Define haemocytes and its types.

Question 3. Explain blood circulation in insect with the help of well labelled diagram.

Question 4. Write short note on haemopoetic organ of insect.

Question 5. Give the function of haemocoel.

UNIT 6: EXCRETORY SYSTEM

CONTENTS:

6.1 Objectives
6.2 Introduction
6.3 Organs of excretion
6.4 Nitrogenous excretion
6.5 Excretory product
6.6 Storage Excretion
6.7 Production of urine and its hormonal regulation
6.8 Terrestrial and salt water insects
6.9 Control of diuresis
6.10 Water Regulation
6.11 Detoxification
6.12 Summary
6.13 Terminal Questions and Answers

6.1 OBJECTIVES

After studying this unit, the students will be able to pursue the knowledge about:

i. Organs of excretion and excretory product
ii. Detail on nitrogenous and storage excretion
iii. Production of urine and its hormonal regulation
iv. Control of diuresis and water regulation in insects
v. Detoxification and its mechanism in insects.
vi. Different habitats of terrestrial and salt water insects.

6.2 INTRODUCTION

In the previous unit, you have read about the insect circulatory system, which involved in a vital physiological process. The blood circulatory system is open in insect. The circulatory system helps in transport of nutrient, hormone and metabolic wastes. The excretion is the process in which an organism eliminates metabolic wastes and unwanted wastes from the excretory system. The nitrogenous waste product is produced in excess which is excreted as uric acid. In insects, the excretory system consists of Malpighian tubules, fat cells, nephrocyte, uricose gland and cuticle. The Malpighian tubules are long, thin, blindly ending tubes arising from the gut near the junction of the midgut and hindgut, and lie freely in the body cavity. They are ectodermal in origin. In some insects, they clearly arise from the midgut, but in others they originate on the anterior part of the hindgut. They open independently into the gut or they may join into an ampulla or a more tubular ureter which then enters into the gut. The wall of the tubule is one cell layer thick with one or a few cells encircling the lumen.

In some insects, there is a muscle sheath associated with the tubules which produce writhing movements within the haemocoel. Outside this is a peritoneal sheath encircling the tubule. It is in the Malpighian tubules, where deamination takes place. Malpighian tubules are absent in the Collembola and aphids, and are represented only by papillae in Diplura, Protura, and Strepsiptera. The number of tubules can be quite variable ranging from 2 in coccids to about

250 in some insects. In many Coleoptera and larval Lepidoptera, the distal parts of the Malpighian tubules are closely associated with the rectum, forming a convoluted layer over its surface. This is known as a cryptonephridial arrangement of the tubules. This arrangement is concerned with improving the uptake of water from the rectum and is absent from most aquatic forms. In some insects (*Periplaneta*), the Malpighian tubules do not contain uric acid, but uric acid granules are present in the wall of the hind intestine and in the contents of the hindgut.

In Thysanura, Dermaptera and Thysanoptera, each Malpighian tubule is made up of secretory and absorptive partfunctional parts. Secretory cells are present in distal part of tubules and absorptive cells are present in proximal part of tubules.Most terrestrial insects produce uric acid as their main nitrogenous waste product. Uric acid is a relatively nontoxic and highly insoluble waste product. Therefore, it can crystallize out of solution, and may be either retained in the body, or eliminated as a solid waste material with little water loss. This is due to uric acid containing less hydrogen per atom of nitrogen than the other two nitrogenous waste substances - the ratio being one hydrogen to one nitrogen. The uric acid collected in the body cell diffuses into blood or haemolymph. In blow fly, allantoin formed by the oxidation of uric acid is found Malpighian tubules.

Nephrocyte and fat body considered as organ of storage excretion. In cockroach,uricose gland acts as storage excretion. These glands store uric acid and discharge it over the spermatophore.The secondary function of Malpighian tubules is regulation of salt and water balance. The tubules are lined with a layer of transport epithelia. These specialized epithelial cells contain pumps that actively transport ions, like sodium (Na+) and potassium (K+), from the hemolymph into the interior of the tubule, called the lumen. Osmosis allows water to follow ions into the tubules passively. From the tubule lumen, water, ions, and waste travel from the intestine to the rectum. Tiny, protruding microvilli lining the inside of the tubules help maximize solute-water coupling and the propulsion of uric acid crystals through the tubules.

In the rectum, specialized glands pump many of the ions back into the hemolymph. Osmosis again allows water to follow ions back into the hemolymph passively. The remaining nitrogenous waste, consisting mainly of concentrated uric acid, can then be excreted from the rectum as a paste or powder, along with faeces. This system of recycling water and ions effectively allows the animal to conserve water in dehydrating environments, such as deserts.Metamorphosis and moulting are controlled by hormones. Moulting is initiated when sensory receptors in the body wall detect the old exoskeleton and activate the production of a hormone from neurosecretory cells in the brain. This hormone acts upon the prothoracic gland, an endocrine gland in the prothorax, which in turn secretes the moulting hormone, a steroid known as ecdysone. Moulting hormone then acts on the epidermis, stimulating growth and cuticle formation. Metamorphosis likewise is controlled by a hormone. Throughout the young larval stages a small gland behind the brain, called the corpus allatum, secretes juvenile hormone (also known as neotenin). As long as this hormone is present in the blood the molting epidermal cells lay down a larval cuticle. In the last larval stage, juvenile hormone is no longer produced, and the insect undergoes metamorphosis into an adult. Among holometabolous insects the pupa develops in the presence of a very small amount of juvenile hormone. Urine production in insect is stimulated by diuretic hormone. Insect cytochrome P450 monooxygenases (P450s) are well known to be involved in metabolic detoxification of xenobiotics, such as phytochemicals, insecticides and environmental pollutants.

6.3 ORGANS OF EXCRETION

In insects, excretory system is well developed for elimination of nitrogenous waste product and maintenance of constant level of salt, water and osmotic pressure of the haemolymph. As a result of protein metabolism, nitrogen is produced in excess which is excreted as uric acid. Thus, insects are uricotelic animals.

The main excretory organ are:

1) Malpighian tubules

2) Fat cells

3) Nephrocytes

4) Uricose gland

5) Cuticle

1) Malpighian tubules

These are the main excretory organs of insects. These are absent in Collembola, some Thysanura and aphids. These are various number of blindly ending tubules. These are the outgrowth of alimentary canal and are attached at the junctions of midgut and hindgut. These are fine, long, unbranched, yellowish coloured tubules present freely in the haemolymph. They are ectodermal in origin. These were first reported by the Italian scientist Marcello Malpighian in 1669 and later named by Meckel (1820) as Malpighian tubules.The walls of Malpighian tubule consist of 4-6 large epithelial cells arranged in a circle which externally rests on the basement membrane.

The number size and modification vary among the insects. Their basic number is considered as 6 but may vary from 2 to 250 and often exist in multiple of 2. These basic number is considered as 6 in Lepidoptera, 6-20 in Ants, 250 in grasshopper, 60 in cockroaches.

On the basis of association of distal end of the tubules with the rectum, two types of excretory system can be recognized.

a) Basic Nephridial system

b) Cryptonephridial system

a) Basic Nephridial system:

In many insects, the distal end of the Malpighian tubules baths freely in the haemolymph of haemocoel. These tubules absorb various waste substances, salt, and water from the haemolymph and discharge into the hind gut. All the tubules open independently but, in some insects, such as gryllids, they open into common ureter which finally opens into gut. Similarly, in some beetles a group of four tubules open into common ampulla while remaining two opens independently.

b) Cryptonephridial system:

In some insects, the distal end of Malpighian tubules is closely associated or inserted into the rectum forming the cryptonephridial system. It is found in the larva of Lepidoptera, Coleoptera, some Hymenoptera and Neuroptera. In Lepidoptera, the tubules typically differentiated into two sections, distal part with fluid and proximal part with sold particles. In Coleoptera, the distal end of the tubules is folded and closely applied to the rectum and both enclosed together by perinephric membrane. This membrane encloses space between the tubules and the rectal wall. The tubules dilate in the perinephric space and the tubules wall thus become very thin and composed of a leptophragma cell. This system helps in the conservation of water and other use full ions by absorbing them from the faecal matter.

Structure of Malpighian tubules:

Each tubule is about 16mm long and 0.5 mm wide and is lined by glandular epithelium. The wall of tubules is composed of 4-6 large epithelial cells arranged in a circle. Each cell bears a brush border or honey comb border towards the lumen. Externally, cell rests on a basement membrane. In Thysanura, Dermaptera and Thysanoptera, each Malpighian tubule is made up of two types of functional parts:

a) Secretory parts- Distal clear region

b) Absorptive parts- Proximal opaque region

Secretory cells are present in distal part of the tubules and made up of dense granular cytoplasm and brush border of 7 to 40μ length cytoplasmic filament separated from each other. Mitochondria are freely distributed in the cell. The distal secretory part extract nitrogenous wastes and water from haemolymph forming a solution called urine. The urine flows towards the proximal absorptive part of tubules.

In insects, like *Rhodnius*, tubules are divided into two parts:

i) Proximal part having brush border it is of 7 to 40μ long cytoplasmic filaments widely separated from each other.

ii) Distal part with honey comb border due to modification of free margin of the cells into 3 to 10μ long cytoplasmic filaments packed very closer together.

The absorptive cell is present in the proximal part of tubules and bears non granular cytoplasm. This part reabsorbs certain salts such as $KHCO_3$ and some water resulting in precipitation of uric acid.

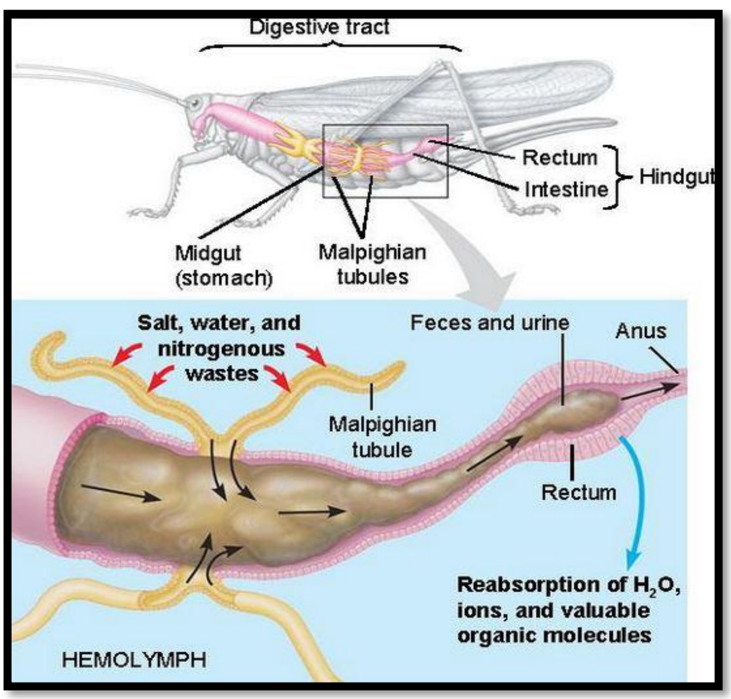

Fig.6.3a: Malpighian tubules of Grasshopper.

Physiology of excretion:

Malpighian tubules are concerned with the removal of metabolic waste from haemolymph. The waste products accumulate around Malpighian tubules and pass into lumen of tubules and are discharged into the hindgut for elimination.

Uric acid, urea and urate are the chief metabolic wastes eliminated by the Malpighian tubules. Allantoin, formed by the oxidation of uric acid is found in the Malpighian of the blow fly. Terrestrial insects are the uricotelic animals like reptiles and birds and their excretory products is uric acid. The uric acid collected in the body cell diffuses into the blood or haemolymph. In blood it combines with Na and $KHCO_3$ to form Na and K urate. These two salts are soluble in water and are easily absorbed by the distal part of Malpighian tubules.

Therefore, uric acid already present in haemolymph combines with reabsorbed $KHCO_3$ and water to form the relatively soluble potassium urate which again transported to lumen of distal portion of Malpighian tubules. These than gradually reach the proximal part. Within the proximal part, by the action of carbonic anhydrase, the urate cell is broken down to produce water, bicarbonate and uric acid. The water and bicarbonate are reabsorbed into the blood and only uric acid is left into the lumen of tubules. From Malpighian tubules, uric acid moves into ileum by peristaltic waves. More water is reabsorbed in colon and rectum so further precipitated more or less solid uric acid is eliminated with faeces through anus.

The habitat of insect determined by the type of excretory end products. Most terrestrial insects are uricotelic while most aquatic insect are ammonotelic, excreting mainly ammonia. The aquatic larvae produce ammonia as its major excretory product, while the terrestrial adults produce uric acid. Excreting uric acid, the insect also conserve water. In some insects, like red cotton bug and blow flies, allantois is formed by the oxidation of uric acid. The meconium of moths and butterflies contains allantoic acid. In *Glossina*, two amino acids arginine and histidine, from the blood of the host are excreted unchanged after absorption. The allantoin, allantoic acid and urea are produced from the breakdown of uric acid. In Collembola, Malpighian are absent, glands in the head open at the base of the labium, and they are concerned in excretion. Other structures of excretory functions are the rectum, fat bodies, urate cells, the hypodermis, cuticle and nephrocytes.

Fat bodies: These are present in all insects and derived from mesoderm of the wall of the embryonic coelomic cavities. It is lobed, white tissue. Since, fat bodies are present in haemocoel, they are immersed in blood. It consists of urate cells. These cells accumulate, produce and store uric acid and urate granules throughout life. This mode of excretion is termed as storage excretion, e.g. Collembola, Hymenoptera larva,Orthoptera,etc. The insect fat body is an organ analogue to vertebrate adipose tissue and liver and functions as a major organ for nutrient storage and energy metabolism. Similar to other larval organs, fat body undergoes a developmental "remodeling" process during the period of insect metamorphosis, with the massive destruction of obsolete larval tissues by programmed cell death and the simultaneous growth and differentiation of adult tissues from small clusters of progenitor cells. Fat body development and function are largely regulated by several hormonal (i.e. insulin and ecdysteroids) and nutritional signals, including oncogenes and tumor suppressors in these pathways.

Nephrocytes:

These are special cells scattered in haemocoel. These are commonly found in strand along each side of the heart and associated with the fat bodies, where they are known as pericardial cell. They are considered as organ of storage excretion. They serve to collect certain complex nitrogenous wastes from the Haemolymph. These wastes are first crystallized, then degraded and the product are held in large vacuoles to be ultimately discharged into haemolymph. They may be very large, as in dipterous larvae, or small and numerous and usually they contain more than one nucleus. They are present on the surface of the heart, or lie on the pericardial septum or the alary muscles. These cells have a deeply invaginated plasma membrane which buds off pinosome into its internal cavity. Nephrocytes also take up dyes and colloidal particles from the haemolymph and also play a role in the control of the heartbeat.

Uricose gland:

In cockroaches, mushroom gland of male possesses long blind tubules at its periphery called uricose gland. These glands store uric acid and discharge it over the spermatophore during copulation. Thus, they work as storage excretion.

Cuticle:

It also acts as a site where nitrogenous waste material is deposited and then eliminated with its shedding at each moult.

6.4 NITROGENOUS EXCRETION

Nitrogenous wastes are formed when proteins are broken down into amino acids for energy. Ammonia is the most basic form of nitrogenous waste and is formed from the remaining amino acids that occur in the breakdown of proteins. Most insects excrete nitrogenous metabolic wastes at some or all stages of their life, although some nitrogen is stored in the fat body or as proteins in the hemolymph in some insects. Many aquatic insects and some flesh-feeding flies excrete large amounts of ammonia, whereas in terrestrial insects wastes generally consist of uric acid and/or certain of its salts (urates), often in combination with urea, pteridines, certain amino acids, and/or relatives of uric acid, such as hypoxanthine, allantoin, and allantoic acid. Amongst these waste compounds, ammonia is relatively toxic and usually must be excreted as a dilute solution, or else rapidly volatilized from the cuticle or faeces (as in cockroaches).It contains a high proportion of hydrogen that can be used in production of water. Urea is less toxic but more soluble, requiring much water for its elimination. Uric acid and urates require less water for synthesis than either ammonia or urea, are non-toxic and, having low solubility in water (at least in acidic conditions), can be excreted essentially dry, without causing osmotic problems.Water conservation is essential for terrestrial insects and uric acid excretion (uricotelism) is highly advantageous.Uric acid and the other nitrogenous waste products are derived from two sources, nucleic acids and proteins. Degradation of nucleic acids is of minor importance; most nitrogenous waste comes from protein breakdown followed by synthesis of hypoxanthine from amino acids. The biochemical reactions that lead to synthesis of this purine appear to be similar to those found in other uric acid-excreting organisms.

The assistance of symbiotic microorganisms, as in cockroaches that house bacteria in their fat body. These cockroaches, including *P. americana*, do not excrete uric acid in the feces even if fed a high-nitrogen diet but do produce large quantities of internally stored urates.

White-pigmented uric acid derivatives colour of the epidermis of some insects and provide the white in the wing scales of certain butterflies (Lepidoptera: Pieridae).Moth *Tineola* and the carpet beetle *Attagenus* excrete large amounts of the sulfur-containing amino acid cystine. Although in tsetse flies, uric acid is the primary excretory product, two amino acids, arginine and histidine, are important components of the urine.

The rate of excretion of uric acid is proportional to the size of the blood meal. The main excretory product of *Glossina morsitans* is uric acid, which makes up more than 60 per cent of the dry wt. of faeces. Arginine, histidine, and haematin are also present in considerable amounts in faecal material; the quantity of each recovered during a starvation cycle is approximately equal to the quantity ingested at the time of feeding. Less nitrogenous waste is eliminated during the first than during subsequent hunger cycles; this difference appears to be a reflection of the use of nitrogenous materials for the synthesis of muscle proteins during the first hunger cycle. Some dipterans metabolize uric acid further to allantoin or urea. Uric acid plays diverse roles as a nitrogenous waste, nitrogen store, pigment, antioxidant and possibly a signaling molecule. Excretion of ammonia by the Malpighian tubules, hindgut, or anal papillae involves multiple transporters, including Na^+/K^+-ATPase, *Rhesus* glycoproteins, ammonia transporters (AMTs) and a hyperpolarization-activated cyclic nucleotide-gated K^+ channel (HCN).

Urate salts provide for temporary storage of monovalent inorganic cations during dehydration in cockroaches and uric acid also be used as an antioxidant to mitigate the effects of reactive oxygen species produced by digestion of the meal in blood-feeding hemipterans. Ammonia is excreted not only by aquatic insects, but also by terrestrial species, including some cockroaches, locusts, fly larvae, and adult mosquitoes. Insects also provide numerous examples of elegant evolutionary solutions to the problem of dietary nitrogen deficiency. Microbial symbionts may fix nitrogen and synthesize essential amino acids which are made available to the host. Larval lepidopterans are also capable of absorption of ammonia from the gut contents, whereas the adults may ingest fluids from sources such as mud puddles or moist ground that provide water, sodium, and nitrogen. Although the Malpighian tubules and hindgut play the dominant role in elimination of excess nitrogen in most species, ancillary structures such as the anal papillae of mosquito larvae are also involved in ammonia excretion.

6.5 EXCRETORY PRODUCT

Insects derive energy by ingesting a wide variety of foods. When these foods are broken down and the nutrients assimilated, there are usually products left over that must be eliminated to prevent them from accumulating. When carbohydrates or lipids are ingested, the energy taken from their oxidation is accompanied by the end products of carbon dioxide and water, neither of which causes any great problems with accumulation or toxicity. Carbon dioxide easily diffuses through insect cuticles or is eliminated through the tracheal system. Excess water is generally not a problem and can be easily eliminated when it accumulates.

In contrast, the metabolism of proteins and nucleic acids produces nitrogen in addition to carbon dioxide and water. Amino acids cannot be stored to as great a degree as carbohydrates and lipids, and when more protein is consumed than is needed for maintenance, the excess nitrogen must be eliminated quickly. The nitrogen itself is not toxic, but in biological systems it readily forms ammonia. Some of this ammonia can be recycled into amino acid synthesis by the formation of glutamate from α-ketoglutarate and glutamine from glutamate, but the excess ammonia that remains is highly toxic unless it is diluted with water. High levels of ammonia can interrupt nervous transmission by substituting for necessary potassium and can also alter carbohydrate and lipid metabolism. Ammonia dissolves easily in water to form ammonium hydroxide, which disrupts cell membrane lipids.

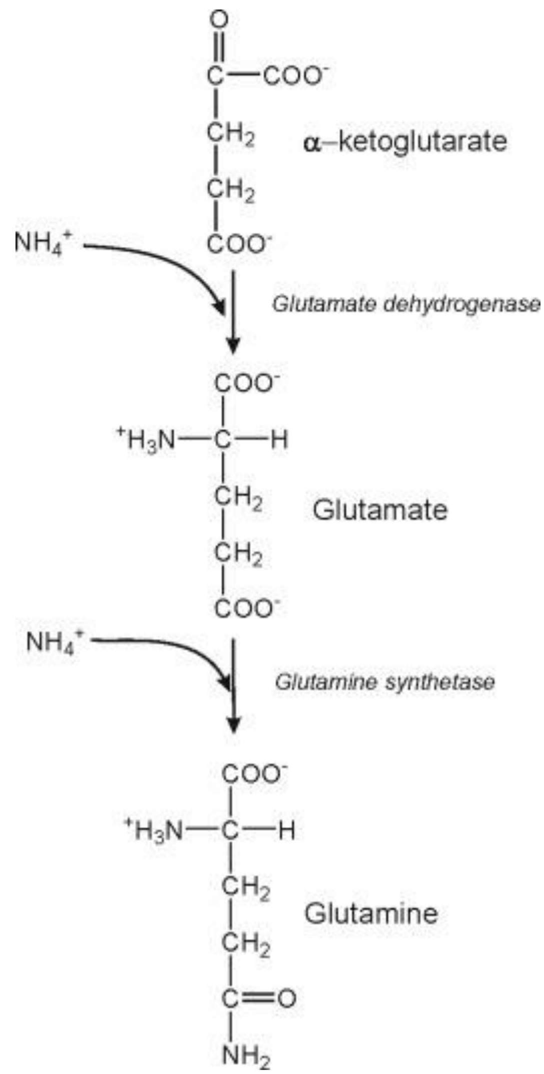

Fig. 6.5a: The incorporation of ammonia in the synthesis of amino acids.

Animals must therefore have excretory systems that are designed to prevent the toxic accumulation of ammonia. Because ammonia is very soluble in water, it is difficult to sequester from critical biological reactions. It crosses biological membranes easily, and concentrations must be maintained below toxic levels by dilution with water. Generally, for each gram of ammonia that is retained within an organism, about 400 ml of water is necessary to reduce it to this safe level. Aquatic insects have little trouble finding these large quantities of water for dilution, and many even excrete the nitrogen from protein metabolism directly as ammonia. However, terrestrial organisms are unable to carry a water supply that is large enough to dilute the ammonia, and there are needs for both water conservation and the incorporation of the nitrogen into a less toxic molecule than ammonia. Most terrestrial organisms have adopted the pathways of incorporating nitrogen into either urea (ureotelic animals) or uric acid (uricotelicanimals). Many mammals possess the enzyme uricase that breaks down uric acid into allantoin, which is much more soluble and easily excreted by the kidneys. In primates, birds, and reptiles, the uricase gene is not expressed, and uric acid remains as the end product of purine metabolism.

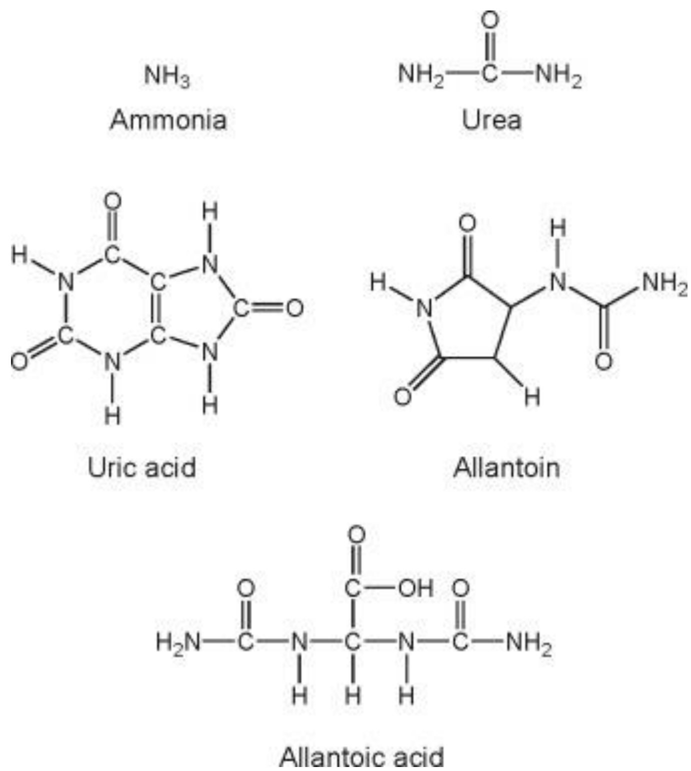

Fig. 6.5b: Excretory molecules that incorporate nitrogen.

As a consequence of their lower toxicity, these molecules can be concentrated in body fluids to a much greater extent than can ammonia and require less water for dilution. Urea is more soluble than ammonia but far less toxic and requires about 10 times less water to be diluted to nontoxic concentrations. For a relatively large terrestrial animal that has easy access to water or that can carry sufficiently large water reserves, urea is an adequate molecule into which the nitrogen may be incorporated. However, in insects, the need for water conservation may have been the driving force for the incorporation of their nitrogen wastes into uric acid, which is an ideal excretory product for small terrestrial animals. Uric acid is highly insoluble in water and therefore fails to reach toxic levels in body fluids, so it requires about 50 times less water to dilute than does ammonia. It is only slightly soluble in biological fluids below pH 7 but becomes much more soluble above pH 9.5, and its insolubility in water allows it to be excreted in a dry form without having a significant effect on water balance. Because hydrogen atoms are derived from water, their loss when incorporated in an excretory molecule affects water balance. Uric acid has the lowest ratio of H : N (1 : 1) for any of the excretory products, compared to the ratio of 2 : 1 for urea and 3 : 1 for ammonia.

The synthesis of uric acid from protein results in the loss of several carbon atoms that could be used for other biosynthesis and requires a substantial amount of energy to build a larger, less toxic molecule. Eight ATP are required to first make the intermediary metabolite, inosine monophosphate (IMP), synthesized by the successive addition of amino groups from glycine, glutamine, and aspartate. The IMP is then converted to uric acid through hypoxanthine and xanthine, the entry points for the catabolism of purines. It has been estimated that when the tsetse fly, *Glossina*, which feeds exclusively on nitrogen-rich blood, ingests a 100-mg meal, it uses the energy from 47 mg of the blood as overhead to dispose of the excess nitrogen through uric acid synthesis and excretion. Other terrestrial organisms can convert uric acid to urea and finally ammonia and carbon dioxide, but insects lack the necessary enzymes.

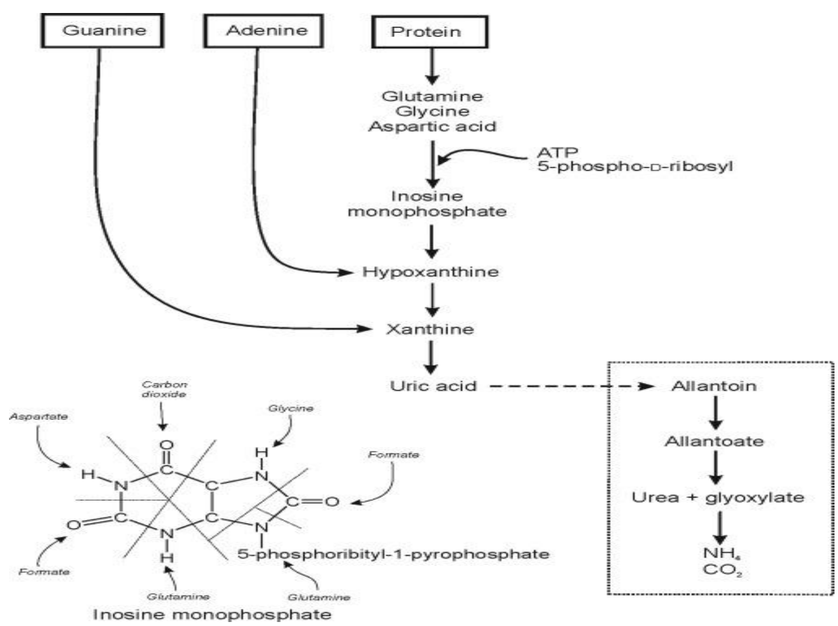

Fig. 6.5c. Pathway for the synthesis of uric acid from nucleic acids and protein.

Inosine monophosphate requires ATP for its synthesis as well as several other building blocks incorporated into the molecule. Not all insects excrete uric acid, and not all excrete one product exclusively. The type of excretory product produced is often a function of diet, developmental stage, and ecological niche. Allantoin is excreted by the hemipteran *Dysdercus*, and certain lepidopterans and larval dipterans excrete allantoic acid. Urea is also a minor component of some insects, but the complete pathway of urea synthesis in insects is not known. Although several enzymes of the ornithine cycle that operates in vertebrates have been identified, evidence for the complete cycle in insects is lacking. Arginine is converted to ornithine and urea by the enzyme arginase, which has been identified in insects, and the amount of urea excreted may correlate with levels of arginine in the diet. So, when insects excrete urea, it may result from the breakdown of dietary arginine. The ammonia that is excreted by some terrestrial insects, including blow fly larvae and some cockroaches and locusts, occurs as a result of the deamination of amino acids and not by the breakdown of urea. In the mosquito, *Aedes aegypti*, abundant nitrogen from blood is ingested each time it feeds, and a proline cycle is utilized to store the ammonia that is derived from amino acid deamination as proline and glutamine, which reduces the excretion of urea and uric acid. The proline can also be used to fuel flight. Ammonia from a blood meal is used to convert glutamate to glutamine. Glutamine and α-ketoglutarate combine to yield two molecules of glutamate: one maintains the cycle and the other is involved in the synthesis of proline.

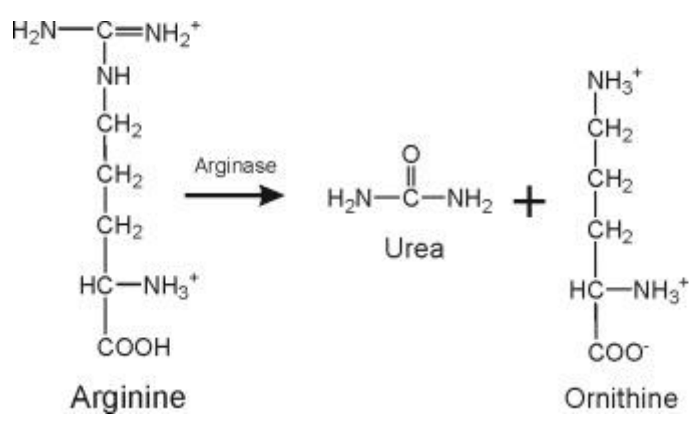

Fig. 6.5 d: One way to account for the release of urea by some insects, with dietary arginine broken down to urea and ornithine.

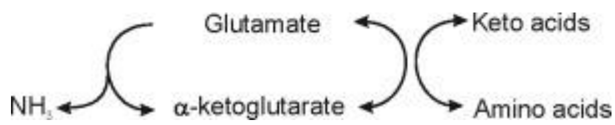

Fig. 6.5 e: The release of ammonia by the deamination of amino acids.

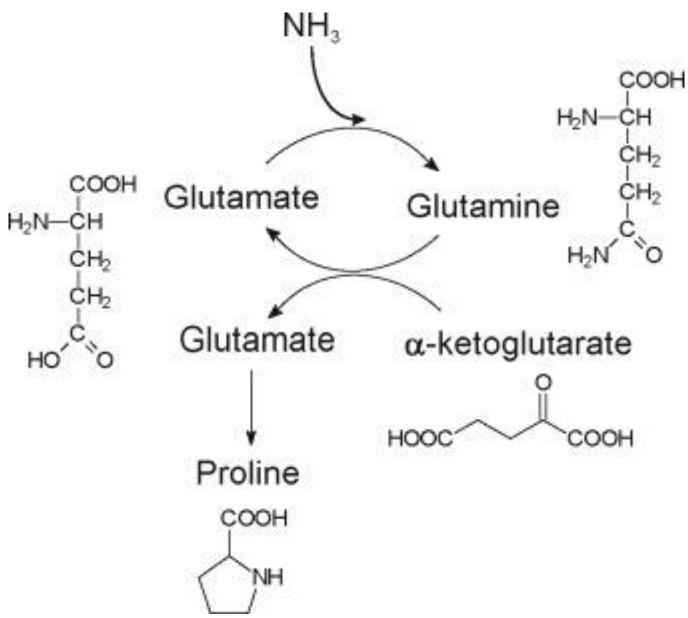

Fig. 6.5 f: The incorporation of nitrogen derived from a mosquito blood meal. Ammonia from the blood meal is used to convert glutamate to glutamine. Glutamine and α-ketoglutarate combine to yield two molecules of glutamate, one of which maintains the cycle and the other is used to synthesize proline.

If the primary urine from the Malpighian tubules was their major excretory product, insects would soon undergo a depletion of their potassium and water. However, superimposed on the excretion by Malpighian tubules is a second system involving the rectum of the hindgut that recovers most of the ions and water, adjusting the excretory product and excreting the secondary urine so that it achieves the necessary osmoregulatory balance for the particular insect.

The rectum comprises the enlarged posterior most section of the hindgut, often containing specialized structures called papillae or rectal pads which are enlarged epithelial cells. Unlike those of the Malpighian tubules, the cells of the rectum lack the infoldings of the basal membrane, but do contain a brush border underneath the cuticle that faces the rectal lumen. Derived from the invagination of epidermal cells, the rectal cells have a cuticular lining on the lumen side that is shed at each molt. Some insects show little in the way of morphological differences that distinguish these rectal pads, and development of the rectum ranges from no modifications in some insects, such as *Drosophila* to the specialized rectal pads present in many orthopterans and coleopterans. Fluid-feeding insects that do not resorb the fluid in their primary urine may not have any rectal pads. The extent to which the recovery of water and ions occurs is determined by the extent to which water must be resorbed, and is a function of environmental and physiological conditions. Insects living under more xeric conditions, such as flour beetles, must resorb more of the water in the hindgut than those living under moister conditions. *Manduca sexta* larvae are able to maintain a steady state and regulate the water content of their bodies based on the water content of the food they ingest, by varying the rate of rectal resorption. Anisopteran dragonflies have tracheal gills in the rectum that are used to extract oxygen from the water.

Because the pH of the rectum is often more acidic than the rest of the hindgut and the solubility of uric acid is considerably reduced under acidic conditions, the acidity in the hindgut precipitates uric acid and allows its excretion to occur in the absence of much water. With its cuticular lining, the rectal epithelium is able to act as a molecular sieve that restricts the passage of larger molecules through the cells. Toxic wastes are retained in the rectal lumen by this lining, and are excreted with little loss of water.

The rectum works in an opposite manner to that of the Malpighian tubules. With the presence of aquaporins, it transports water and ions from the material within the gut lumen into the hemolymph. An electrogenic Cl^- pump on the lumen side of the cell membrane that is not coupled to any other ions drives the resorption process, moving Cl^- from the gut lumen into the hemolymph. A Na/K-ATPase mediates the transport of sodium into the hemolymph and generates a positive electrical potential on the hemolymph side of the membrane, and also drives fluid transport. Chloride exits the cell passively into the hemolymph through cAMP-stimulated channels, and potassium also follows passively by an electrical coupling with potassium channels.

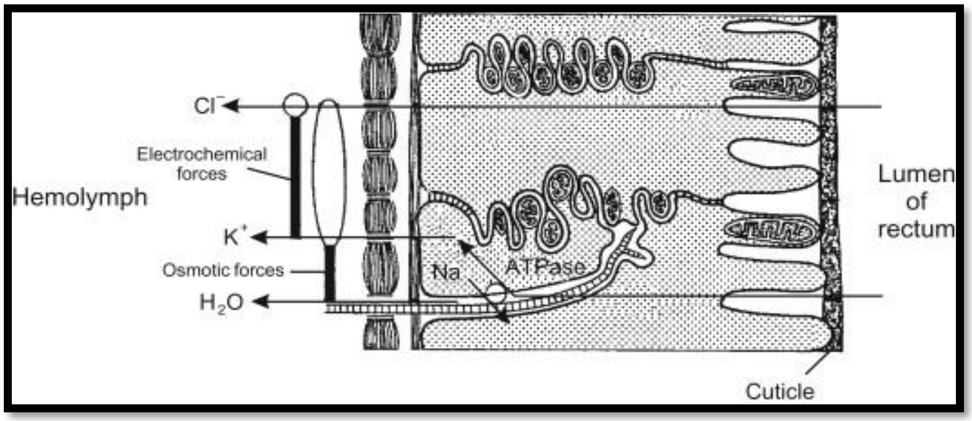

Fig. 6.5g. A rectal cell and its ion transport.

6.6 STORAGE EXCRETION

Some insects, such as the silverfish, springtails and aphids have no Malpighian tubules. Stick insects may have three types of Malpighian tubules. In addition to excretion by Malpighian tubules, insects often exhibit storage excretion in which waste materials are sequestered safely and retained inside special storage cells. For example, the fat body may contain urate cells which accumulate urate crystals throughout the life of the insect.

The excretory waste materials are retained within the body in different sites. In American cockroach, uric acid is stored as urates in the cells of fat body whereas in red cotton bug, uric acid is stored in the body wall, giving white colour. Uric acid is stored in the male accessory glands to produce the outer coat of spermatophore, which is excreted during copulation. In Pierid butterflies, it is stored in the wing scales giving white colour. Waste products of pupal metabolism (Meconium) is stored and released during adult emergence.The fat body plays major roles in the life of insects. It is a dynamic tissue involved in multiple metabolic functions. One of these functions is to store and release energy in response to the energy demands of the insect. Insects store energy reserves in the form of glycogen and triglycerides in the adipocytes, the main fat body cell. Insect adipocytes can store a great amount of lipid reserves as cytoplasmic lipid droplets. Lipid metabolism is essential for growth and reproduction and provides energy needed during extended nonfeeding periods.

Uric acid storage in the epidermal cells of *Manduca sexta.* In the integument of *Manduca sexta* (L.) larvae, uric acid is shown to be preferentially stored within the white pigmented epidermal cells. Uric acid concentrations in the epidermal tissues are higher in the dorso-lateral white stripes (>500 nmol/mg) than in adjacent blue-green pigmented regions (30 nmol/mg). The distribution and temporal movements of uric acid were determined by feeding larvae artificial diet containing [^{14}C] hypoxanthine for the first 48 h of the fifth instar. Day-3 larvae (86 h after larval ecdysis) contained label mainly in the white-pigmented epidermal tissues with only small quantities in the gut and no radioactivity in the fat body or haemolymph. For day-4 larvae, about 80% of the label in the epidermis was either translocated to storage within fat body or excreted before the onset of wandering. HPLC analysis and reactivity with uricase confirmed that the labelled material in the tissues was uric acid. Ultra-structurally, the white-pigmented epidermal cells contain an abundance of lightly-stained urate granules, which unite into large accumulations toward the basal side of cells during the initial stages of metamorphosis.

An alternative strategy to the removal of wastes through the Malpighian tubule-rectum system used by some insects is storage excretion, the retention of the wastes in "out of the way places" within the body. Adult Lepidoptera convert much of their waste nitrogen into pteridines that are stored in the integument, eyes, or wing scales, giving the insects their characteristic colour patterns. In the larval stages of many species uric acid crystallizes out in ordinary fat body cells and epidermis, even though the Malpighian tubules are functional. It appears that this is caused by the metabolic activity of the cells themselves (i.e., they are not accumulating uric acid from the hemolymph), and crystallization occurs by virtue of the particular conditions (pH, ionic content, etc.) existing in the cells. During the later stages of pupation, the crystals disappear, the uric acid apparently having been transferred to the meconium (the collective wastes of pupal metabolism, released at eclosion) via the excretory system. It is worth noting that in many species the Malpighian tubules are entirely reconstituted during the pupal stage. Thus, storage of uric acid in fat body and epidermal cells is of great importance at this time. Yet other insects, notably termites and cockroaches, retain large quantities of uric acid in special cells (urocytes) within the fat body.

6.7 PRODUCTION OF URINE AND ITS HORMONAL REGULATION

Diuretic hormones generally act on the Malpighian tubules to stimulate urine production Antidiuretic hormones generally increase fluid reabsorption by act on the hindgut. Malpighian tubules are not innervated;thus, they must be regulated by hormones released in the blood

Muscles of the tubules can be modulated by diuretic hormones and Myotrophic peptides. Increase writhing movement in hemolymph.

Transport mechanisms and their control in various segments of insect excretory systems are reviewed and compared to those of vertebrate nephrons, exocrine glands, and hindguts. Formation of the primary urine in most insect Malpighian tubules (MT) is by isosmotic secretion, which is driven by an apical cation (K+) pump rather than by Na+-K+-ATPase. Unlike the glomerular filtrate of vertebrates, insect MT fluid is very different from the blood in composition, often having very high K+-to-Na+ ratios, and urine-to-plasma values much less than unity for most other solutes. The total surface area of insect MT is some 20 times that of vertebrate glomeruli per unit body weight. Secretion of MT fluid is regulated by neuropeptides over a wide range of rats, similar to glomerular filtration rate values for many vertebrate kidneys. Several secretory mechanisms for selected solutes are probably common to insect and vertebrate tubules. Unlike vertebrates, insects usually reabsorb most of the filtered water, ions, and metabolites in the rectum, which has a small surface area relative to the MT. The rectum is also where ionic and osmotic composition of the excreta is finally adjusted, under the control of neuropeptide hormones. In the rectum, insect excreta can become as hyperosmotic as mammalian urine, even though a countercurrent multiplier system is not present. Active transport of Cl- predominates in both locust rectum and the thick ascending limb of Henle's loop, but the characteristics of the anion transfer process are quite different in these two epithelia.

The diverse excretory systems of insects exhibit several features that appear unusual when comparisons are made with the mammalian kidney. Secretion by the Malpighian tubules of a fluid that is unlike the blood in composition, substitutes for glomerular filtration. Various reabsorptive functions, such as volume reduction, regulation of individual electrolytes, adjustment of osmotic concentration and pH regulation, which are associated with distinct renal segments in the mammalian kidney, all occur simultaneously in the rectum of terrestrial insects. Involvement of an extracellular molecular sieve in selective reabsorption is novel. As far as water transport is concerned, the rectal pads of the cockroach and locust appear to accomplish, across a single layer of cells, the same function as the countercurrent multiplier system of the mammalian kidney with its several epithelial layers. Direct absorption of water vapour in the rectum of some insects from atmospheres of low relative humidity, clearly involves quite different and unknown mechanisms. Finally, saline-water insect larvae produce hyperosmotic excreta by direct secretion of ions into the rectal lumen. They can adjust individual transport processes to form various secretions, which are appropriate to the natural waters of diverse chemical types in which these larvae thrive.

Insects require diuretic hormones (DH) to control rate of urine production by Malpighian tubules. There are 13 similar DH related to CRF, but with far more diverse structures than the CRF superfamily. It has become apparent that many species have two DH which are related but belong to sub-families of paralogues. The kinins are another family of small peptides that control diuresis. They share a rather conserved C-terminal Penta peptide motif and have been found to have synergistic effects with the CRF-like DH in several species of insect. *R. prolixus* and *Manduca sexta*; these insects represent species with disparate dietary habits, the former being an obligate blood feeder and the latter being phytophagous.

6.8 TERRISTRIAL AND SALT WATER INSECTS

Terrestrial insects have a huge impact on human society, both as crop, veterinary, and human pests and as disease vectors. In addition, they are an essential part of the ecosystem as detritivores, scavengers, pollinators, and biological control agents. They also play a major role in human medicine, in recreational hobbies, and in the arts as well as providing direct aesthetic benefits. Terrestrial insects, like their freshwater counterparts, are also used by conservation biologists as indicators of ecosystem health or biodiversity. Terrestrial insect populations and communities make excellent models for basic ecological studies because they are present in virtually every habitat on the planet, including the Antarctic, and they fill every feeding society in a community. The importance of their ecological roles influence ecosystem processes and functions such as decomposition, primary production, and nutrient cycling.

Terrestrial insects spend most of their life on land. They get into the water only by coincidence. Blowy conditions and other natural conditions can cause these insects to sometimes lose their caution and end up becoming a meal for a trout. It would be a rare occasion that trout ever became selective on any terrestrial insect. It would be possible during a flying ant fall, or possibly when a large number of ants or beetles were washed into the water by heavy rains or high winds. This means that most all of the time, the trout are just looking for something to eat on the surface of the water. They do not recognize the various types or species of terrestrial insects that may come floating by. They firmly feed opportunistically on them. When there are few insects on the water trout are likely to take every insect that comes by.

If a large amount of any one insect became available over a period of time, then it would be likely that the trout would search only for that insect or feed selectively on it. When this happens, they begin to settle into a steady feeding rhythm and focus on individual insects. Facts are, it would be rare that enough terrestrial insects fell, blew or got washed into the water to cause selective feeding.

Insects feed on every sort of organic matter, and their methods of feeding and digestion have become modified accordingly. The major climatic hazards faced by terrestrial insects are temperature extremes and desiccation. Different species function best at various optimal temperatures. If conditions are too hot, an insect seeks out a cool, moist, and shady spot. If exposed to the sun on a hot day, an insect will position itself so as to present the smallest amount of body surface to the heat. If conditions are too cool, insects will remain in the sun to warm themselves. Many butterflies must spread their wings and expose the large surface to the sun like solar collectors to warm the flight muscles before they can fly. Many moths can raise their temperature by vibrating their wings or "shivering" before taking flight. The heat generated in this way is conserved by hairs or scales that maintain an insulating layer of air around the body. The optimum muscle temperature for flight is from 38 to 40 °C (100 to 104 °F).

In extremely cold weather the danger for insects is freezing, and insects that survive winters in cold latitudes are called cold hardy. A few insects (e.g., some caterpillars and aquatic midge larvae) tolerate ice formation in body fluids, although it is probable that the cell contents do not freeze. In most insects, however, cold hardiness means resistance to freezing. This resistance results partly from accumulation of large quantities of glycerol as an antifreeze and partly from physical changes in the blood that permit supercooling to temperatures far below the freezing point of water without the blood freezing.

Preventing water loss is another important aspect of life in terrestrial environments. All insects have a waxy (lipid) layer that coats the outer surface of the exoskeleton to prevent water loss from the body wall. In addition, most terrestrial insects also have adaptations to avoid water loss through respiration and waste elimination.

These are some common terrestrial insects that get into the freestone streams of Yellowstone National Park.

Beetles:

The most common terrestrial insect in the park is the beetle or Coleoptera. There are both aquatic and terrestrial forms of beetles but here we are concerned with the terrestrial form. Some species of beetles can fly and these are more likely to get into the water than the others that cannot fly. Overhanging limbs of trees, grass and shrubs provide the places for beetles to fall into the water.

Ants:

Ants, the Formicidae family of insects, is one of the next most plentiful terrestrial insects found in the park. Fast rising water caused by heavy rains is responsible for ants and terrestrial beetles getting into the water more than anything else. Ants live in colonies and when they do get washed into the water, they usually do so in large quantities.Some ants can fly and these flying ants can easily end up in the water. When they do, they are usually preyed on by trout in a feeding frenzy. These great swarms of arts perform their nuptial flights, the winged males or drones, die shortly after they swarm. If the flight of ants happens over a stream they fall in the water and usually just carpet the water.

Grasshoppers:

Grasshopper exist on every stream in the park but they are not as plentiful in the forest as they are in the streams that flow through meadows and open areas where high grass exist.Wherever find banks with lots of grass there most likely are lots of grasshoppers. Grasshoppers become important starting in July but much more so in the latter part of the summer and early autumn.

Bees:

Bees live in colonies. These colonies are usually very large and contains thousands of insects. They sometimes fall into the water.Major changes required for life in an aquatic habitat include modifications of the legs for swimming and adaptations for respiration. Most aquatic insects swim using the second or third (or both) pairs of legs. In some, the distal (away from the body) leg segments may simply be flattened and serve as oars. In others, there is a row of movable hairs on these segments that fold against the leg to offer less resistance during the forward stroke and then extend out, forming an oar like surface during the power stroke. In some, like the water striders (Gerridae), long thin legs allow them to “walk” on the surface film of ponds and streams.

To breathe, some insects simply rise to the water surface and take atmospheric air into their tracheal systems. Mosquito larvae use only the last pair of abdominal spiracles, which open at the tip of a respiratory siphon. Water beetles (e.g., *Dytiscus*) have converted the space between the protective sheaths on the hind wings (elytra) and the abdomen into an air-storage chamber. Air-breathing insects can prolong the period of submergence by trapping air among their surface hairs. This air film acts as a physical gill and makes possible oxygen uptake from water. Other adaptations to an aquatic environment have occurred in larvae that obtain all their oxygen directly from the water. In midge larvae, abundant tracheae (breathing tubes) contact the entire thin cuticle. Caddisfly (Trichoptera) and mayfly (Ephemeroptera) larvae have tracheal gills on the abdomen or thorax. In dragonfly larvae, the gills are inside the rectum, and the water is pumped in and out through the anus, whereas damselflies have external rectal gills.

Defense from enemies: Insects may originate some protection from the horny or leathery cuticle and also have various chemical defenses. Few caterpillars have special irritating hairs, which break up into barbed fragments that contain a poisonous substance which causes intense itching and serves as a protection against many birds.Dermal glands of many insects discharge repellent or poisonous secretions over the cuticle, whereas others are protected by poisons that are present continuously in the blood and tissues. Such poisons often are derived from the plants on which the insects feed. In many hymenopterans (ants, bees, wasps), accessory glands are present in the female reproductive system have become modified to produce toxic proteins. These poisons, injected into the nervous system of the prey, paralyze it. In this state the prey serves as food for the wasp larva. Stings are also used by hymenopterans, including ants, wasps, and bees, for self-defense.

Fig 6.8a:Leaf Insect.

Fig6.8b:Caterpillars

Source: https://www.insectomania.org/compound-eyes/brackishwater-and-saltwater-insects.html

Concealment is an important protective device for insects. For some, this may be accomplished by simply hiding beneath stones or the bark of trees. However, many species rely on some forms of protective coloration. Protective coloration may take the form of camouflage (cryptic coloration) in which the insect blends into its background. The coloration of many insects copies a specific background with extraordinary detail. Stick insects (*Carausius*) can change their colour to match that of the background by moving pigment granules in their epidermal cells. Some caterpillars also have patterns that develop in response to a background, although these are irreversible. Insects such as caterpillars, which rely on cryptic coloration, often combine it with a rigid deathlike position.Alternatively, insects that have well-developed chemical defenses generally show conspicuous warning (aposematic) coloration. Experiments have proved that predators, such as birds quickly learn to associate such coloration “labels” with nauseous or dangerous prey. Finally, insects without nauseous qualities may gain protection by mimicry—developing a conspicuous colour pattern similar to that found in distasteful species.

The habitat occupied by brackish-water and saltwater insects can vary widely in ionic content and osmotic pressure. During periods of warm, dry weather the salinity may increase several folds. Conversely, after heavy rains or the melting of snow in spring, the salinity may approach that of fresh water. It is not surprising, therefore, to find experimentally that such insects can regulate their hemolymph osmotic pressure over a wide range of external salt concentrations (Figure 6.8c). Larvae of *Aedes detritus* and *Ephydrariparia*, inhabitants of salt marshes, can survive in media containing the equivalent of 0 to about 7-8% sodium chloride. Over this range of concentration, the hemolymph osmotic pressure changes by only 40-60 %.

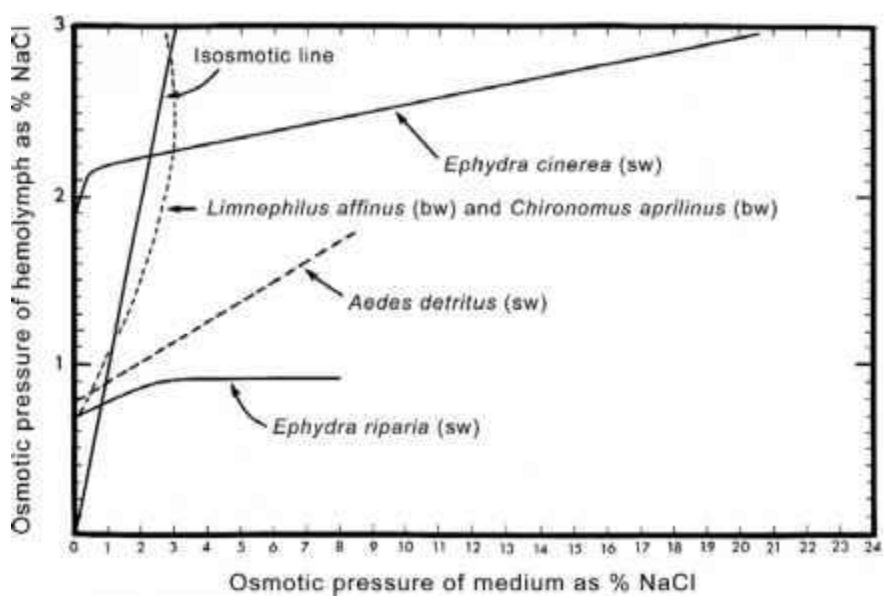

Fig 6.8c. The relationship between osmotic pressure of the hemolymph and that of the external medium in some saltwater (sw) and brackish-water (bw) larvae.

6.9 CONTROL OF DIURESIS

In the case of *Rhodniusprolixus*, the diuretic hormones act on the midgut to stimulate the absorption of fluid from the blood meal into the insect's hemolymph and simultaneously act upon the Malpighian tubules to stimulate fluid secretion. Serotonin is a true diuretic hormone in *Rhodniusprolixus* and tyramine, synthesized by the principal cells of the Malpighian tubules in *Drosophila melanogaster* has diuretic activity with actions on the stellate cells. Serotonin is a true diuretic hormone in *R. prolixus*, released into the hemo-lymph at gorging, and stimulating distal Malpighian tubule secretion by 1000folds via a cAMP-dependent mechanism, and stimulating proximal tubules to reabsorb KCl. Serotonin is released rapidly into the hemolymph immediately after the onset of gorging and initiates diuresis. Termination of diuresis is necessary to avoid excessive loss of water and salts, thereby maintaining volume, ionic, and osmotic stability of the hemolymph.

Insects, because of their small size and high surface area: volume ratios, face formidable problems of water and ion balance. Water loss is minimized by a number of physical and behavioural mechanisms, but ultimately the homeostatic maintenance of the internal milieu is dependent upon the control of excretion. In every species which has been studied, hormones which affect diuresis have been reported. These hormones, usually low molecular weight peptides, may enhance fluid loss (diuretic hormone) or retard it (antidiuretic hormone). The application of very sensitive analytical techniques, such as high-performance liquid chromatography (HPLC) to the study of diuretic hormones/antidiuretic hormones has indicated that they are widely distributed throughout the insect central nervous system, although the most concentrated source, and presumably the main site of release, is the corpus cardiacum. HPLC techniques have also revealed that many species contain more than one diuretic hormone, with each acting via a different second messenger system and exerting different effects on the Malpighian tubules. The integrated action of multiple diuretic hormones, and the overall integration of the secretory and reabsorptive segments of the excretory system, represent one of the more interesting and least well understood aspects of the endocrine control of excretion.

Primary urine production in insect Malpighian tubules is stimulated by two classes of neuropeptides, CRF-related diuretic peptides and insect kinins. The CRF-related peptide of the locust, *Locustamigratoria*, has a hormonal role in the control of post feeding diuresis, but the functional role of the kinins has yet to be defined. The two classes of peptide act synergistically to stimulate tubule secretion, and the kinins may therefore have a modulatory action in the control of diuresis. The peptides differ in their effects on Malpighian tubule ion transport, and this could be important for the regulation of hemolymph volume and composition.

Rhodniusprolixus eliminates NaCl-rich urine at high rates following its infrequent but massive blood meals. This diuresis involves stimulation of Malpighian tubule fluid secretion by diuretic hormones released in response to distention of the abdomen during feeding. The precipitous decline in urine flow that occurs several hours after feeding has been thought until now to result from a decline in diuretic hormone release. The insect cardio acceleratory peptide 2b (CAP2b) and cyclic GMP are part of a novel mechanism of anti-diuresis. Secretion rates of 5-hydroxytryptamine-stimulated Malpighian tubules are reduced by low doses of CAP2b or cyclic GMP. Maximal secretion rates are restored by exposing tubules to 1 mmol l-1 cyclic AMP. Levels of cyclic GMP in isolated tubules increase in response to CAP2b, consistent with a role for cyclic GMP as an intracellular second messenger. Levels of cyclic GMP in tubules also increase as urine output rates decline *in vivo*, suggesting a physiological role for this nucleotide in the termination of diuresis.

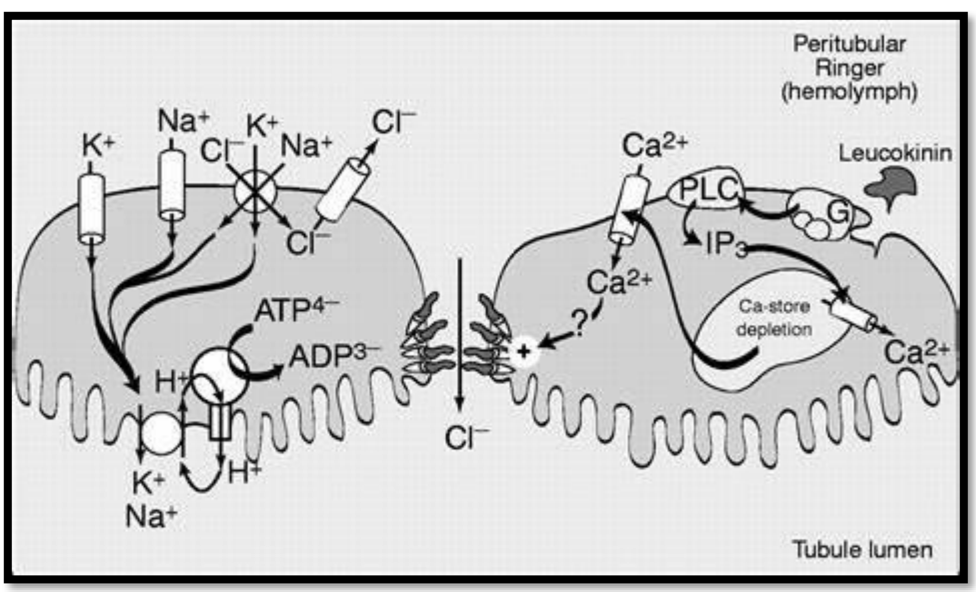

Fig.6.8d Transport mechanism of diuresis in Malpighian tubules of insect.

6.10 WATER REGULATION

In insects, the water and ion balance are control by hormones. Insects are found in different habitats ranging from the driest deserts to aquatic habitats of diverse ionic composition. In many species, the environment changes dramatically during metamorphosis. Insects respond to perturbations in body water composition by using a combination of hormonal and autonomous mechanisms to vary the amount and composition of fluid excreted by the excretory system. Hormones acting on the hindgut seem to stimulate recovery of fluid and ions from the primary urine, leading to cycling of materials through the excretory system and hemolymph, and clearance of wastes. The majority of information about regulation of hindgut transport comes from studies on the locust. The locust hindgut consists of two distinct regions, a more anterior ileum and a more posterior rectum. Two peptide factors isolated from the corpus cardiacum are ion transport peptide, acting on the ileum, and chloride transport-stimulating hormone, acting on the rectum. Other factors that stimulate water reabsorption by the hindgut include neuroparsins. A and B. In addition, a number of factors modulate contractions by the hindgut musculature.

In insects, the regulation of water balance is important in maintaining homeostasis. Homeostasis is the state of relative stability of the internal environment of an organism. One of the main processes involved in the control of water balance is diuresis. Diuresis is the elimination of excess water in the form of urine. This secretion takes place within the excretory system of the insect, which includes the Malpighian tubules and the hindgut. Excretion and water balance are under neuroendocrine control. Insect diuretic hormones play key roles in the regulation of water balance. Diuretic hormones are involved in the process of diuresis. They are responsible for stimulating the secretion of urine by the Malpighian tubules. There are three primary diuretic hormones found in insects: CRF-like diuretic hormones, kinins, and serotonin. They are generally released in response to feeding, which involves a large uptake of water. This is particularly important for blood-eating insects, such as *Rhodniusprolixus* (blood-sucking bug) and *Aedes aegypti* (yellow fever mosquito), which can consume up to 10-20X their body weight during a single meal. Among the three main insect diuretic hormones, two are classified as neuropeptides (CRF-like DH and kinins) and one as a neurotransmitter (serotonin, 5-HT). All three stimulate the secretion of urine by the Malpighian tubules, but each has its own way of mediating this excretion. When presented together, these diuretic hormones can act in synergism to further enhance the process of diuresis.

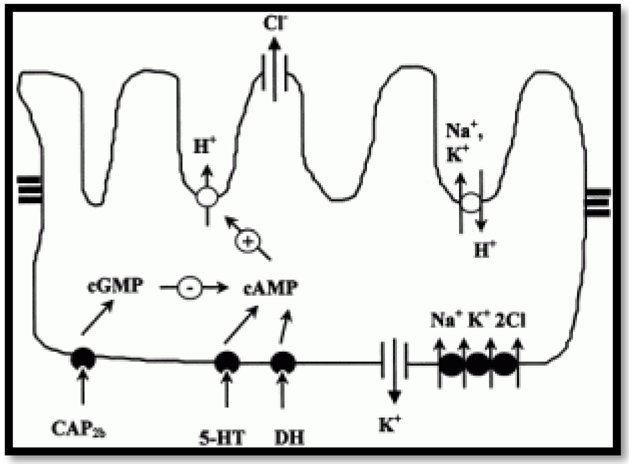

Fig.6.10 a. Regulation of water balance.

CRF-like diuretic hormones mediate the secretion of urine through the production of cyclic AMP. These cAMP act as secondary messengers to mediate the secretion of urine by the Malpighian tubules. The CRF-like DH via cAMP, promotes the active transport of Na^+ and K^+ ions into the Malpighian tubule lumen. This transport of ions from the hemolymph (blood analogue for insects) to the tubule lumen is the driving force for the secretion of urine (Beyenbach, K.W. 1995). Although CRF-like DH is present in the majority of insects, each species of insects may have its own specific CRF-like DH. Some examples of CRF-like DH include: Locusta-DH in locusts, Acheta-DH in crickets, Stomoxys-DH and Musca-DH in flies, *Periplaneta*-DH in cockroaches, and *Manduca*-DH in moths. In addition, some species of insects possess two CRF-like DH, such as Manduca sexta, which has Manduca-DH I and Manduca-DH II.

In majority of insects, kinin family of neuropeptides is found. Like CRF-related diuretic hormone, kinins also stimulate the secretion of urine. However, unlike CRF-related DH which act via cAMP, kinins mediate the excretion of urine by increasing the levels of intracellular $Ca^{2.}$ Some examples of insect kinins include: leucokinins in Leucophaeamaderae (cockroach), achetakinins in *Acheta domesticus* (cricket). In plant-feeding insects such as locusts and moths, which consume a diet rich in K^+ with relatively little Na^+. Another difference between CRF-like DH and kinins is that CRF-like DH stimulates the active transport of cations (Na^+; K^+), while kinins stimulate the passive transport of anions (Cl^-).

6.11 DETOXIFICATION

Detoxification is a process of removing toxic substance or waste substance from body. Insects are faced with numerous toxins (xenobiotics) as they go through life, some produced naturally by plants (sometimes called allelochemicals) and some produced by humans (insecticides). To survive the natural toxins, insects have evolved various detoxification mechanisms. These same mechanisms also sometimes allow insects to overcome insecticides, and the level and type of mechanisms differ greatly. This results in differing toxicity among different stages, populations, and species of insects. Insect cytochrome P450 monooxygenases (P450s) are well known to be involved in metabolic detoxification of xenobiotics, such as phytochemicals, insecticides and environmental pollutants. Enhanced metabolic detoxification is closely associated with the constitutive overexpression and induction of P450s. In general, multiple insect P450s are co-responsible for xenobiotic detoxification. Considering the capacity of P450s to respond to a wide range of xenobiotics, synergistic interactions between natural and synthetic xenobiotics and P450-mediated cross-tolerance/resistance are ubiquitous. Recent studies have indicated that both transcription factors and signaling pathways are involved in the regulation of P450 genes in xenobiotic responses.

Detoxification can be divided into two phases. Phase I (primary) and phase II (secondary) processes. Phase I reactions consist of oxidation, hydrolysis and reduction. The phase I metabolites are sometimes polar enough to be excreted, but usually are further converted by phase II reactions. In phase II reactions, the polar products are conjugated with a variety of endogenous compounds such as sugars, sulfate, phosphate, amino acids or glutathione, and subsequently excreted. Phase I reactions are responsible for decreasing biological activity of a toxicant and therefore the enzymes involved are rate limiting with respect to toxicity.

A).Phase I Reactions

1. Oxidation -The oxidative reactions are carried out by a group of enzymes called microsomal cytochrome P450 monooxygenases [also known as mixed-function oxidases (MFO) or microsomal oxidases]. These enzymes, located in the endoplasmic reticulum of eukaryotic cells, commonly are found in mammals, birds, reptiles, fish, crustaceans, molluscs, insects, bacteria, yeast and higher plants. Microsomal monooxygenases are a three-component system comprised of cytochrome P450, NADPH-cytochrome P450 reductase and a phospholipid.

2. Epoxidation - Epoxidation is an important microsomal reaction. For example, the cyclodiene insecticide aldrin can be oxidized to its epoxide dieldrin, which is more environmentally persistent than its precursor. Epoxides are usually highly unstable and can undergo rapid enzymatic hydration to dihydrodiols catalyzed by epoxide hydrolases. These highly reactive epoxides can form adducts with cellular macromolecules such as proteins, RNA and DNA, often resulting in chemical carcinogenesis.

3. Hydroxylation - Hydroxylation can occur with an aliphatic or aromatic carbon atom. DDT and the carbamate insecticide carbaryl are known to be hydroxylated by microsomal monooxygenases. Microsomal hydroxylation usually results in detoxification.

4. N-Dealkylation - N-Dealkylation is a common reaction in the metabolism of xenobiotics including organophosphorus and carbamate insecticides. The reaction is believed to proceed by an unstable α-hydroxy intermediate which spontaneously releases an aldehyde in the case of the primary alkyl group. For example, the carbamate insecticide propoxur is N- demethylated to 2-isopropoxyphenyl carbamate via 2-isopropoxyphenyl N- hydroxymethyl carbamate. Microsomal N-dealkylation results in detoxification.

5. O-Dealkylation - O-Dealkylation of alkyl groups of the ester or ether structures of insecticides occurs frequently but it also involves an unstable α-hydroxy intermediate as found in N- dealkylation. For example, methoxychlor is O- demethylated by the system. O- Dealkylation is known to occur with a wide variety of organophosphates including certain dimethyl triesters. O-Dealkylation results in detoxification.

6. Desulfuration -Organophosphorus insecticides with the P = S group are desulfurated by microsomal monooxygenases of insects to their corresponding P = O analogues. This reaction results in activation because the product, P = O, binds more tightly to the acetylcholinesterase and are thus more potent acetylcholinesterase inhibitors.

7. Sulfoxidation - Many thioether-containing insecticides such as organophosphorus compounds and carbamates are oxidized by microsomal monooxygenases of insects to their corresponding sulfoxides. In general, sulfoxide formation represents an oxidative activation process leading to an increase in anticholinesterase activity. For example, phorate is oxidized to phorate sulfoxide. In the fall armyworm, *Spodopterafrugiperda*, sulfoxidation of phorate requires NADPH and is inhibited by carbon monoxide and piperonyl butoxide, and induced by cytochrome P450 inducers (e.g., indole 3-carbinol and indole 3-acetonitrile).

8. Reduction - Although insects contain reductases catalyzing the reduction of xenobiotics, reduction is less common than oxidation. Three types of reduction reactions, i.e., nitro reduction, azo reduction, and aldehyde/ketone reduction are known to occur in insects. An NADPH-dependent nitro reductase has been reported in the soluble fraction (cytosol) of adult female houseflies which reduces parathion to amino parathion. The reductase activity is not affected by the presence of oxygen. Nitrobenzene reductase activity has been detected in the fat body, gut and Malpighian tubules of the Madagascar cockroach, *Gromphadorhinaportentosa*. Anaerobic conditions are essential for activity. The enzymes in the microsomes are strongly NADH dependent, whereas those in the soluble fraction are strongly NADPH dependent.

9. Hydrolysis - Insecticides such as organophosphates, carbamates, pyrethroids and some juvenoids, which contain ester linkages, are susceptible to hydrolysis. Esterase are hydrolases that split ester compounds by the addition of water to yield an acid and an alcohol. Esterases which metabolize organophosphates can be divided into three groups: A-esterases are not inhibited by organophosphates but hydrolyze them; B-esterases are susceptible to organophosphate inhibition; and C-esterases which are uninhibited by organophosphates but do not degrade them. There carboxylesterases and phosphatases (also called phosphorotriester hydrolases) are two types of esterases that are important in metabolizing insecticides. Carboxylesterases which are B-esterases play significant roles in degrading organophosphates, carbamates, pyrethroids and some juvenoids in insects. The best example is Malathion hydrolysis, which yields both α- and β- monoacids and ethanol.

B) Phase II Reactions - Phase I reactions with xenobiotics result in the addition of functional groups such as hydroxyl, carboxyl, and epoxide. The phase I products can undergo further conjugation reactions with endogenous molecules. These conjugations are called phase II reactions. The endogenous molecules include sugars, amino acids, glutathione, phosphate and sulfate. Conjugation products usually are more polar, less toxic and more readily excreted than their parent compounds. Three types of conjugation reactions occur in insects. Type I requires an activated conjugating agent which then combines with the substrate to form the conjugated product. Type II involves the activation of the substrate to form an activated donor which then combines with an endogenous molecule to yield a conjugated product. In type III, conjugation can proceed directly between the substrate and conjugating agent without involving activation. Thus, types I and II require formation of high energy intermediates before conjugation reactions proceed. The chemical groups required for type I are OH, NH_2, COOH and SH (glucose conjugation, sulfate conjugation and phosphate conjugation); for type II, COOH (amino acid conjugation); and for type III, halogens, alkenes, NO_2, epoxides, ethers and esters (glutathione conjugation).

1. Glucose conjugation - Glucose conjugation is found commonly in insects and plants but rarely in mammals. Glucoside formation is accomplished by a reaction between an activated intermediate, uridine diphosphate glucose (UDPG), and the xenobiotic, with the enzyme glucosyl transferase as catalyst. In insects, O-glucosides have been identified from some insecticide metabolism studies, including carbaryl, propoxur, carbofuran, DDT and allethrin.

2. Sulfate conjugation - Sulfate conjugation requires the prior activation of inorganic sulfate by adenosine triphosphate to an active intermediate, 3'-phosphoadenosine- 5'-phosphosulfate (PAPS), from which the sulfate group is transferred to a substrate (ROH). The final step is catalyzed by an enzyme called sulfotransferase.

3. Phosphate Conjugation - Conjugation of xenobiotics with phosphate is rare in animals. Insects and arachnids are the major groups of animals in which phosphate conjugation has been demonstrated. Phosphate conjugates have been detected in houseflies, blow flies (*Luciliasericata*) and New Zealand grass grubs (*Costelytrazealandica*) when treated with 1-naphthol, 2-naphthol or p- nitrophenol. An active phosphotransferase prepared from the gut of the Madagascar cockroach requires ATP and Mg+ for phosphorylation of p-nitrophenol.

4. Amino acid Conjugation - Aromatic acids often are conjugated with amino acids in animals, glycine being the most frequently used amino acid. Conjugation of aromatic acids with glycine has been demonstrated in several species of insects. Glycine conjugation occurs in two steps. The first involves the activation of the substrate (RCOOH) by an enzyme system requiring ATP and coenzyme A and the second the condensation of the activated substrate with glycine.

5. Glutathione Conjugation - Glutathione conjugation is performed by a group of multifunctional enzymes known as glutathione S-transferases. Glutathione S-transferases are important in the metabolism of organophosphorus insecticides resulting in detoxification. For example, methyl parathion is dealkylated by glutathione S- transferase to form desmethyl parathion and methyl glutathione. On the other hand, parathion can be dearylated by glutathione S-transferase to produce diethyl phosphorothioic acid and S-(p- nitrophenyl) glutathione. Interestingly, a glutathione S-transferase isozyme isolated from the housefly exhibits DDT-dehydrochlorinase activity.The haem detoxification in insect. Haem is involved in many biological reactions, including oxygen transport, respiration and photosynthesis. In Free State, however, haem can generate reactive oxygen species that can damage biological molecules. It can also disrupt the phospholipid bilayer of cell membranes. In *Plasmodium* parasites, which are the aetiological agents of malaria disease, up to 80% of host-cell haemoglobin is digested, leaving the free haem group to be detoxified in the parasite's food vacuole by polymerizing it into a harmless dark-brown crystalline structure called malaria pigment or haemozoin. Haem detoxification is also a challenge for blood-sucking insects, which digest several times their own weight of vertebrate blood during a blood meal.

The insect gut microbiota has been shown to contribute to the host's digestion, detoxification, development, pathogen resistance, and physiology. The weevil plays a pioneering role in diet digestion and mainly digests macromolecules into smaller molecules which are then mainly digested by gut bacteria.

The activity of Detoxification Enzymes in Aquatic and Terrestrial Insects. They summarized six different detoxification enzymes including general esterase, permethrin hydrolase, total cytochrome P-450, aldrin epoxidase, and glutathione transferase measured with two different substrates were recorded from a variety of terrestrial and aquatic insects. Aquatic insects generally exhibited a well-developed detoxification enzyme system and often displayed activities equal to or greater than those of the terrestrial species tested.

6.12 SUMMARY

In insects, elimination of nitrogenous waste product through excretory system. The main excretory organ are Malpighian tubules, fat cells, nephrocytes, uricose gland and cuticle.Malpighian tubules are the main excretory organs of insects. These are absent in Collembola, some Thysanura and aphids. These are the outgrowth of alimentary canal and are attached at the junction of midgut and hindgut. They are ectodermal in origin. The number size and modification vary among the insects. Their basic number is considered as 6 but may vary from 2 to 250 and often exist in multiple of 2. These basic number is considered as 6 in Lepidoptera, 6-20 in Ants, 250 in grasshopper, 60 in cockroaches. In Thysanura, Dermaptera and Thysanoptera, each Malpighian tubule is made up of two types of functional parts, viz. Secretory parts- Distal clear region, and Absorptive parts- Proximal opaque region. Secretory cells are present in distal part of the tubules and made up of dense granular cytoplasm and brush border of 7 to 40µ length cytoplasmic filament separated from each other. The absorptive cells are present in the proximal part of tubules and bears non granular cytoplasm. This part reabsorbs certain salts such as KHCO3 and some water resulting in precipitation of uric acid.Uric acid, urea and urate are the chief metabolic wastes eliminated by the Malpighian tubules. Allantoin, formed by the oxidation of uric acid, is found in the Malpighian of the blow fly. The uric acid collected in the body cell diffuses into the blood or haemolymph. In blood, it combines with Na and $KHCO_3$ to form Na and K urate. These two salts are soluble in water and are easily absorbed by the distal part of Malpighian tubules. The habitat of insect determined by the type of excretory end products. Most terrestrial insects are uricotelic while most aquatic insect are ammonotelic, excreting mainly ammonia. In some insects, like red cotton bug and blowflies, allantois is formed by the oxidation of uric acid. The meconium of moths and butterflies contains allantoic acid. Fat body derived from mesoderm of the wall of the embryonic coelomic cavities. It is lobed, white tissue. Since fat body present in haemocoel they are immersed in blood. Nephrocytes are special cells scattered in haemocoel. They are considered as organ of storage excretion. They serve to collect certain complex nitrogenous wastes from the haemolymph. Uricose gland store uric acid and discharge it over the spermatophore during copulation. Thus, they work as storage excretion. Cuticle also acts as a site where nitrogenous waste material is deposited and then eliminated with its shedding at each moult.

Many aquatic insects and some flesh-feeding flies excrete large amounts of ammonia, whereas in terrestrial insects wastes generally consist of uric acid and/or certain of its salts (urates), often in combination with urea, pteridines, certain amino acids, and/or relatives of uric acid, such as hypoxanthine, allantoin, and allantoic acid. Water conservation is essential for terrestrial insects and uric acid excretion (uricotelism) is highly advantageous.Uric acid and the other nitrogenous waste products are derived from two sources, nucleic acids and proteins. Ammonia is excreted not only by aquatic insects, but also by terrestrial species, including some cockroaches, locusts, fly larvae, and adult mosquitoes. Insects also provide numerous examples of elegant evolutionary solutions to the problem of dietary nitrogen deficiency.

Urea is more soluble than ammonia but far less toxic and requires about 10 times less water to be diluted to nontoxic concentrations. In insects, the need for water conservation may have been the driving force for the incorporation of their nitrogen wastes into uric acid, which is an ideal excretory product for small terrestrial animals. Uric acid is highly insoluble in water and therefore fails to reach toxic levels in body fluids, so it requires about 50 times less water to dilute than does ammonia. It is only slightly soluble in biological fluids below pH 7 but becomes much more soluble above pH 9.5, and its insolubility in water allows it to be excreted in a dry form without having a significant effect on water balance. Allantoin is excreted by the hemipteran,*Dysdercus*, and certain lepidopterans and larval dipterans excrete allantoic acid. Arginine is converted to ornithine and urea by the enzyme arginase, which has been identified in insects, and the amount of urea excreted may correlate with levels of arginine in the diet. So, when insects do excrete urea, it may result from the breakdown of dietary arginine. Gut bacteria may contribute to the varied excretory products of insects, but this is difficult to evaluate unless the insects are reared aseptically. Ammonia from a blood meal is used to convert glutamate to glutamine. Glutamine and α-ketoglutarate combine to yield two molecules of glutamate: one maintains the cycle and the other is involved in the synthesis of proline.

The excretory waste materials are retained within the body in different sites. In American cockroach, uric acid is stored as urates in the cells of fat body, whereas in red cotton bug, uric acid is stored in the body wall, giving white colour. Uric acid is stored in the male accessory glands to produce the outer coat of spermatophore, which is excreted during copulation. In Pierid butterflies, it is stored in the wing scales giving white colour. Waste products of pupal metabolism (Meconium) is stored and released during adult emergence.Formation of the primary urine, in most insect Malpighian tubules, is by isosmotic secretion, which is driven by an apical cation (K+) pump rather than by Na+-K+-ATPase. Insects have low pressure circulatory systems and require diuretic hormones (DH) to control rate of urine production by Malpighian tubules. There are 13 similar DH related to CRF, but with far more diverse structures than the CRF superfamily. Primary urine production in insect Malpighian tubules is stimulated by two classes of neuropeptides, CRF-related diuretic peptides and insect kinins.

Terrestrial insects are an essential part of the ecosystem as detritivores, scavengers, pollinators, and biological control agents. Their populations and communities make excellent models for basic ecological studies. They also play a major role in human medicine, in recreational hobbies, and in the arts as well as providing direct aesthetic benefits. Terrestrial insects, like their freshwater counterparts, are also used by conservation biologists as indicators of ecosystem health or biodiversity. The most common terrestrial insect in the park is the beetle or Coleoptera. There are both aquatic and terrestrial forms of beetles but here we are concerned with the terrestrial form. The habitat occupied by brackish-water and saltwater insects can vary widely in ionic content and osmotic pressure. During periods of warm, dry weather the salinity may increase several folds. Larvae of *Aedes detritus* and *Ephydrariparia*, inhabitants of salt marshes, can survive in media containing the equivalent of 0 to about 7-8% sodium chloride.

In insects, the water and ion balance are control by hormones. The regulation of water balance is important in maintaining homeostasis. One of the main processes involved in the control of water balance is diuresis. Diuresis is the elimination of excess water in the form of urine. This secretion takes place within the excretory system of the insect, which includes the Malpighian tubules and the hindgut. Excretion and water balance are under neuroendocrine control. Insect diuretic hormones play key roles in the regulation of water balance. They are responsible for stimulating the secretion of urine by the Malpighian tubules. There are three primary diuretic hormones found in insects: CRF-like diuretic hormones, kinins, and serotonin. They are generally released in response to feeding, which involves a large uptake of water. In majority of insects, kinin family of neuropeptides is found. Like CRF-related diuretic hormone, kinins also stimulate the secretion of urine. CRF-like DH stimulates the active transport of cations (Na^+; K^+) while kinins stimulate the passive transport of anions (Cl^-).

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6.13 TERMINAL QUESTIONS AND ANSWERS

Question 1. Describe the physiology of excretion in insect**.**

Question2. Define nitrogenous and storage excretion**.**

Question 3. Explain the production of urine and its hormonal regulation**.**

Question 4. Define detoxification and its mechanism in insect**.**

Question 5. Write a short note on terrestrial insects and salt water insects.

UNIT – 7 RESPIRATORY SYSTEM OF INSECTS

Contents:

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7.3 Types of Respiratory Organs

7.4 Structure and Functions of Various Respiratory Organs

7.5 Respiratory System and its Modifications

7.6 Respiration in Terrestrial, Aquatic and Endoparasitic Insects

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7.1 OBJECTIVES

After going through this unit you will be able to explain that

- Different organs associated with respiratory system.
- Function of hemolymph and mechanism of respiration.
- Various adaptations of different insects living under different habitat.
- How parasitic forms cope up with environment?
- What is the importance of hemolymph?

7.2 INTRODUCTION

During gas exchange, an insect's respiratory system introduces respiratory gases into its interior. Insects enter their respiratory systems through spiracles, which are external openings. In some insects, these external openings act as muscular valves that lead to the internal respiratory system, which consists of a dense network of tubes called tracheae. Through this network of transverse and longitudinal tracheae, pressure is equalized throughout the body.

As a waste product of cellular respiration, it removes carbon dioxide (CO_2) that is produced as a waste product of oxygenation. Insects (and many other arthropods) have a separate respiratory system from their circulatory system.

7.3 TYPES OF RESPIRATORY ORGANS

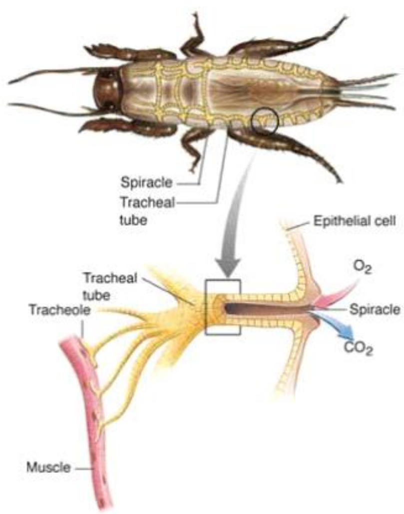
SPIRACLES:

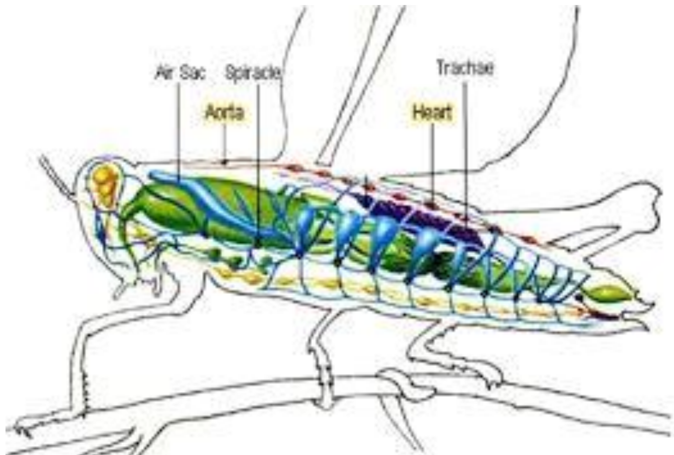
Spiracles have a chamber or atrium that has a valve that opens and closes. As a result, air passage is regulated and water loss is minimized. A peritreme is a sclerotized cuticular plate that surrounds each spiracle. As invaginations of the epidermis, tracheae have a continuous lining with the body cuticle. The spiral ridges called taenidia give the tracheae a ringed appearance.

Tracheae are flexible but resist compression because of this. When an insect moults, its cuticular linings are shed, but its tracheole linings are not.

TRACHEOLES:

Tracheoles have a diameter of less than 1 micrometer. They end blindly and are in close contact with respiring tissues. There is no taenidia or waxlayer. Gases can pass through the cuticulin layer. Intracellular in nature, it is enclosed only in the cytoplasm of tracheal cells and tracheoblasts. There are four tracheal trunks in the trachea, namely lateral, dorsal, ventral, and visceral, which help in the passage of air. In the trachea, there are thin walled-collapsible sac-like dilations, called airsacks, in which taenidia do not exist. Oxygen is stored in air sacs. Insects that fly and swim need buoyancy. Ensure that organs can grow. Insulates heat and acts as a sound resonator.





Respiratory System of Insect

7.4 STRUCTURE AND FUNCTIONS OF VARIOUS RESPIRATORY ORGANS MECHANISM OF RESPIRATION

As oxygen passes through the tracheae and the tracheoles, it passes into target cells through ventilation and diffusion along a gradient of concentration. While oxygen molecules move inwards in the tracheal system (Inspiration), CO_2 and water vapour molecules move outwards (Expiration).

THE TRACHEAL SYSTEM

Tracheae : The tracheae are the larger tubes of the tracheal system, running inwards from the spiracles and usually breaking into finer branches the smallest of which are about 2 microns in diameter. Tracheae are ectodermal in origin and as such have a cuticular lining which is shed during each molt. A spiral thickening of the intima runs along each tube, each ring of the spiral being called a taenidium. The taenidia prevent the collapse of the trachea if the pressure within is reduced. The intima consists of a layer of cuticulin, forming the surface lining the lumen, and a protein/chitin layer on the outside.

Air-sacs - In places tracheae are expanded to form thin-walled air-sacs in which the taenidia are absent or poorly developed. Consequently the air-sacs will collapse under pressure and they play a very important part in ventilation of the tracheal system as well as having other functions. Air-sacs occur in many insects.

Tracheoles - These are the smaller branches of the tracheal system. There is no clear distinction between the tracheae and the tracheoles but the tracheoles are always intracellular and retain their cuticular lining at molting. Proximally the tracheoles are about 1 micron in diameter, tapering to about 0.1 micron distally. They are formed in cells called **tracheoblasts** which are derived from the epidermal cells lining the tracheae. The tracheoles are very intimately associated with the tissues and in fibrillar muscle they may indent the muscle plasma membrane and penetrate deep into the fiber, but it is probable that they never truly become intercellular. Distally the tracheoles end blindly or they may anastomose.

Distribution of the tracheal system - The tracheal system arises externally at the spiracles. In many of the Apterygota (except Lepismatidae) the tracheae from each spiracle form a series of unconnected tufts. But in most insects the tracheae from neighboring spiracles anastomose to form longitudinal trunks running the length of the body. Usually there is a lateral trunk on either side of the body and these are often the largest tracheae. Also there is often a dorsal and a ventral longitudinal trunk. The longitudinal tracheae are often connected to those of the other side of the body by transverse commissures, while smaller branches extend to the various tissues which give rise to the tracheoles which run to the cells.

The arrangement of the tracheal system varies in different insects, but in general the heart and dorsal muscles are supplied by branches from the dorsal trunks; the alimentary canal, gonads, legs and wings from the lateral trunks; and the central nervous system from the ventral trunks or transverse commissures. The head is supplied from spiracle 1 through 2 main tracheal branches on each side, a dorsal branch to the antennae, eyes, and brain, and a ventral branch to the mouthparts and their muscles. In some insects the connecting tubes are constricted which somewhat isolates the tracheal system of the head from the rest of the body ensuring a good supply of oxygen to the brain and major sense organs. Accordingly, the pterothorax in some insects also has its tracheal system somewhat isolated from the rest.

SPIRACLES:

The spiracles are the external openings of the tracheal system. They are lateral in position, usually on the pleura, and, except in *Japyx* (Diplura) which has 2 pairs of spiracles on the metathorax, there are never more than one pair per segment. Often the spiracle is contained in a small, distinct sclerite, the peritreme.

Number and distribution of spiracles - With the exception of some Diplura, the largest number of spiracles found in insects is 10 pairs, 2 thoracic and 8 abdominal, and the respiratory system can be classified on the basis of the number and distribution of the functional spiracles:

1. **Polypneustic** - at least 8 functional spiracles on each side:

a. **Holopneustic** - 10 spiracles - 1 mesothoracic, 1 metathoracic, 8 abdominal - as in bibionid

larvae.

b. **Peripneustic** - 9 spiracles - 1 mesothoracic, 8 abdominal - as in cecidomyid larvae.

c. **Hemipneustic** - 8 spiracles - 1 mesothoracic, 7 abdominal - as in mycetophilid larvae.

2. **Oligopneustic** - 1 or 2 functional spiracles on each side:

a. **Amphipneustic** - 2 spiracles - 1 mesothoracic, 1 post-abdominal - as in psychodid larvae.

b. **Metapneustic** - 1 spiracle - 1 post-abdominal - as in culicid larvae.

c. **Propneustic** - 1 spiracle - 1 mesothoracic - as in dipterous pupae.

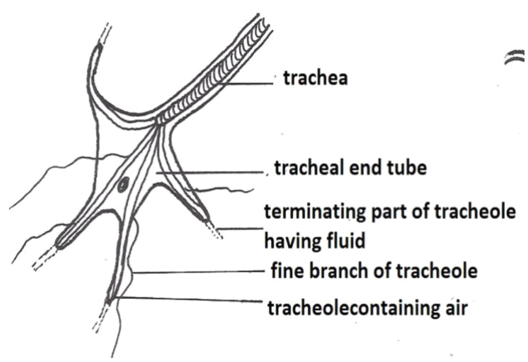
3. **Apneustic** - no functional spiracles - as in chironomid larvae.

Apneustic does not mean that the insect has no tracheal system, but rather that the tracheal system does not open externally.

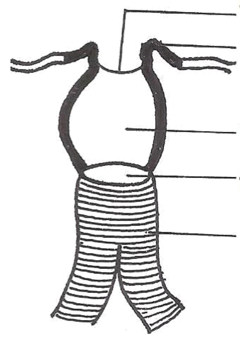
Structure of the spiracles - In its simplest form, in the Apterygota, the spiracle is a direct opening from the outside to the tracheae, but generally the visible opening leads into a cavity, the atrium, from which the tracheae arise. In this case the opening and the atrium collectively are called the spiracle. Often the walls of the atrium are lined with hairs which filter out the dust. In other insects there may be a sieve plate with small pores which filters out the dust.

The spiracles of most terrestial insects have a closing mechanism which is important in the conservation of water. The closing mechanism may consist of 1 or 2 movable valves in the spiracular opening itself or it may be internal, closing off the atrium from the tracheae by means of a constriction.

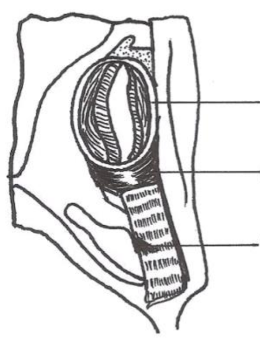
Spiracle 2 in the grasshopper occurs in the membranous area between the meso- and metathorax. It is closed by 2 movable semicircular valves which are unsclerotized except at the hinge and are thickened basally to form a pad into which a muscle is inserted. The muscle, by pulling down on the valves, causes them to rotate and so to close. The spiracle usually opens simply from the elasticity of the surrounding cuticle. This one-muscle type of spiracle is usually found on the thorax, but in Orthoptera spiracle 1 has both an opener muscle and a closer muscle. This spiracle occurs in the membranous area between the pro and mesothorax, and consists of a fixed anterior valve and a movable posterior valve. It is unusual in having 2 orifices which lead directly from the external opening.



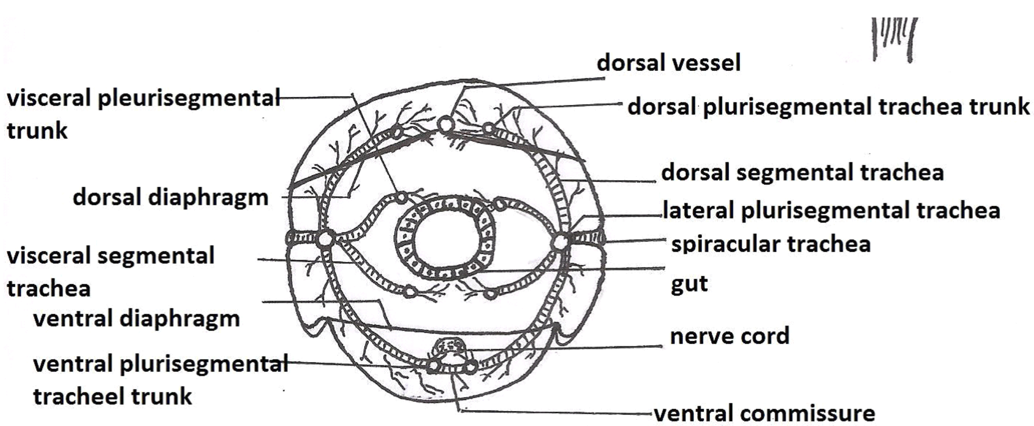
Tracheole



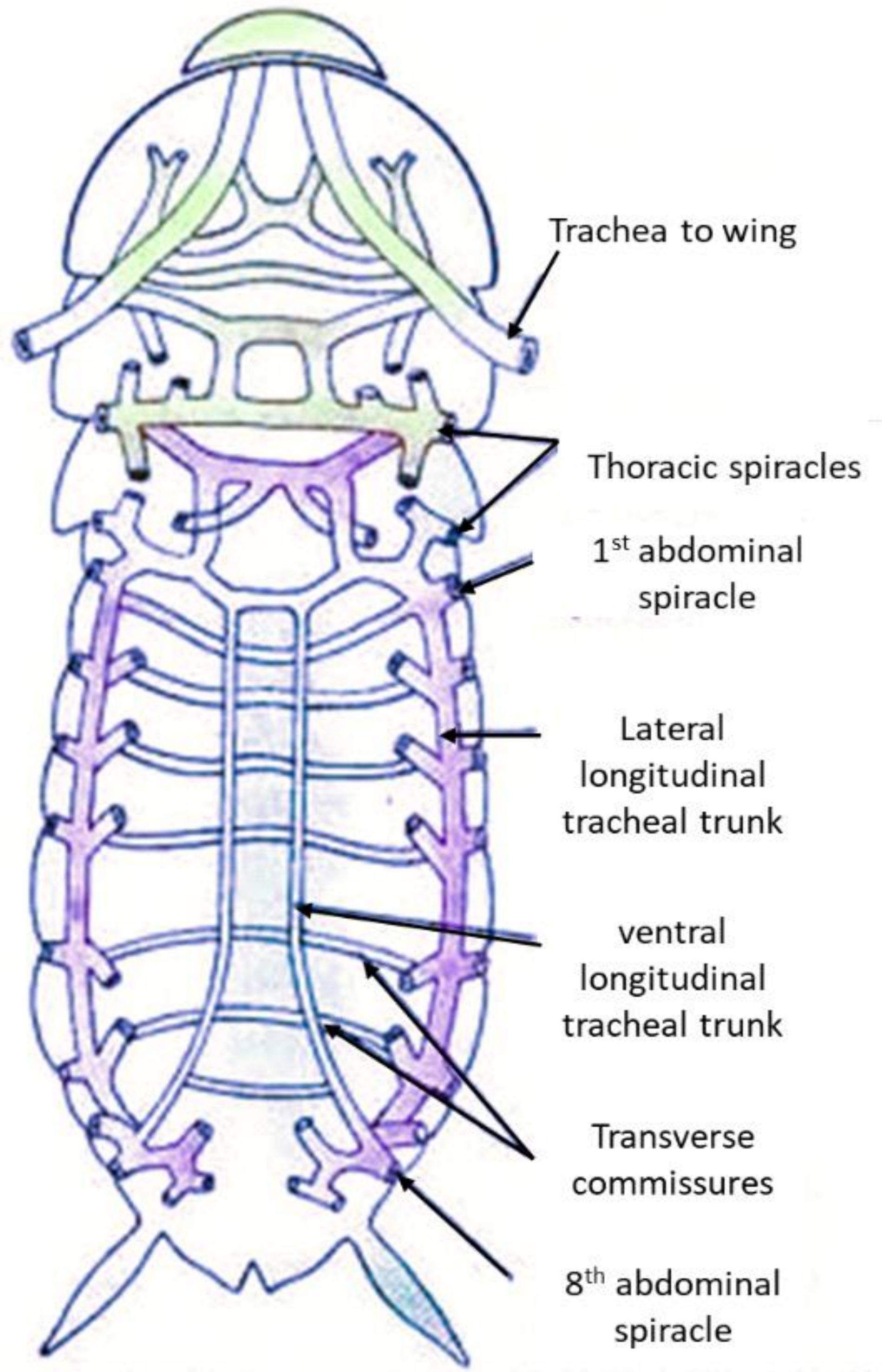
Spiracle



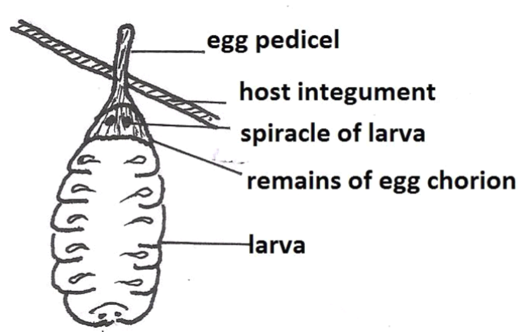
Outer and inner view of 2nd thoracic spiracle of grasshopper



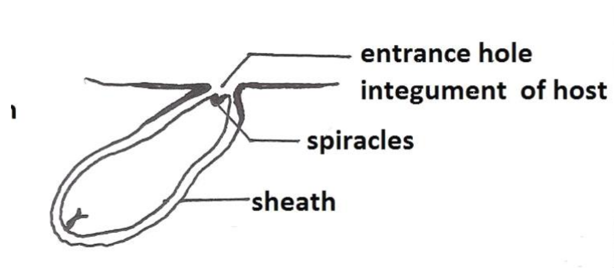
T.S. of generalized insect through abdomen showing main tracheal trunks



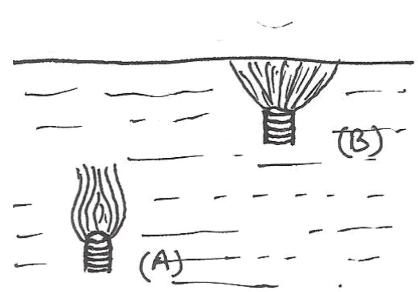
L.S. of generalized insect showing main tracheal trunks and spiracles



Larva of Blastothrix (Hymenoptera)



Larva of Thrixion (Diptera)



A) Hydrofuge hair around spiracle in submerged stage, B) on water surface

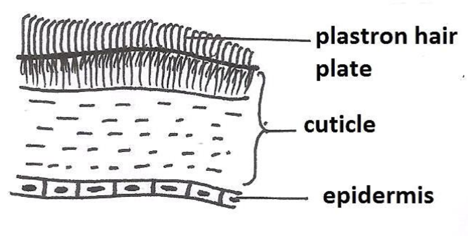


Diagram showing plastron hair for respiration

Control of spiracle opening - The spiracles are normally open for the shortest time necessary for efficient respiration in order to keep water loss from the tracheal system to a minimum. Spiracle closure results from the sustained contraction of the closer muscle, while opening commonly results from the elasticity of the surrounding cuticle when the closer muscle is relaxed. The muscle is controlled by the central nervous system, but may also respond to local chemical stimuli which interact with the central control.

7.5 RESPIRATORY SYSTEM AND ITS MODIFICATIONS

CUTANEOUS RESPIRATION

Some gaseous exchange takes place through the cuticle of most insects, but this does not amount to very much of the total respiration. On the other hand, Protura and most Collembola have no tracheal system and must depend on cutaneous respiration together with transport from the body surface to the tissures by the haemolymph. Cutaneous respiration is also important in eggs, aquatic insects, and endoparasitic insects.

OTHER FUNCTIONS OF THE TRACHEAL SYSTEM

The whole tracheal system, and in particular the air-sacs, lowers the specific gravity of the insect. In aquatic insects, but not in terrestrial ones, it also gives some degree of buoyancy which can be adjusted. Expansion of the tracheal system may assist in inflation of the insect after a molt. Some air-sacs near the flight muscles are thought to aid in cooling of the muscles during periods of high activity. There is an air chamber in cicadas that functions as a resonating chamber to help amplify its call.

7.6 RESPIRATION IN TERRESTRIAL, AQUATIC AND ENDOPARASITIC INSECTS RESPIRATION IN TERRESTRIAL INSECTS

The respiratory organs of terrestrial insects consist of tracheal tubes with external spiracular valves that control gas exchange. Despite their relatively high metabolic rate, many insects have highly discontinuous patterns of gas exchange, including long periods when the spiracles are fully closed.

RESPIRATION IN AQUATIC INSECTS

Aquatic insects obtain oxygen from the air or from air dissolved in the water. Most get their oxygen directly from the air. This usually requires periodic visits to the surface. A few insects, however, maintain a semipermanent connection with the air via a long respiratory siphon or through the aerenchyma of certain aquatic plants. Insects returning to the surface face 2 main problems. First they must be able to break the surface film of the water, and secondly they must be able to keep the water from entering the spiracles once they re-enter the water. Respiration by aquatic insects usually requires one of the following modifications:

1. **Tracheal gills** - Evaginated trachea or tracheoles. Found in immatures (Stoneflies, Mayflies, some Odonata).

2. **Rectal gills** - Found in Odonata. Inside the rectum there are 5 tracheoles, water is taken into the rectum, the oxygen is removed, and then the water is expelled.

3. **Spiracular gills** - Found in aquatic Diptera. Often are insects that are associated with streams that periodically dry up. When in water they function as gills. If stream dries up part of the gills break off leaving a hole so air can enter directly.

4. **Respiratory tubes** - Found in Nepidae (water scorpions). Simply is a siphon or respiratory tube.

5. **Post-abdominal Siphon** - Found in mosquitoes. This is a posterior sharp siphon that is used to pierce the plant tissue to obtain oxygen.

6. **Air bubble** - Found in aquatic Hemiptera and Coleoptera. The insect captures a bubble of air at surface and carries it below surface and use it to breathe. Sometimes the oxygen diffuses from the water directly into the air bubble.

7. **Plastron respiration** - This is called a hydrofuge and consists of special hairs which trap a bubble. The hairs prevent the bubble from collapsing. The insect can stay underwater with 1 bubble for up to 4 months.

RESPIRATION IN ENDOPARASITIC INSECTS

The majority of endoparasites obtain some oxygen by diffusion through the cuticle from the host tissues. Other insects, and particularly older, actively growing larvae, communicate with the outside air either through the body wall of the host or via its respiratory system. The majority of these insects are metapneustic or amphipneustic, using the posterior spiracles to obtain their oxygen.

HAEMOGLOBIN

Most insects have no respiratory pigments, but a few have haemoglobin in solution in the blood. The best known examples are the aquatic larvae of *Chironomus* and related insects, the aquatic bug *Anisops*, and the endoparasitic larvae of *Gasterophilus* (Diptera). The molecular weight of the haemoglobin in insects is about half that found in vertebrates indicating that insect haemoglobin probably consists of only 2 haem groups.

7.7 AQUATIC RESPIRATORY ADAPTATIONS

1. Closed tracheal system

In some aquatic and many endoparasitic larvae spiracles are absent and the tracheae divide peripherally to form a network. This covers the body surface, allowing cutaneous gas exchange. e.g. Gills : Tracheated thin outgrowth of body wall.

Lamellate gills - mayfly naiad

Filamentous gills - damselfly naiad

Rectal gills - dragonfly naiad

2. Open tracheal system

i. Air store: Air bubble stored beneath wings acts as physical gill, e.g. water bug.

ii. Respiratory siphon - e.g. Wriggler

iii. Caudal breathing tube -e.g. Water scorpion

iv. Plastron: Closely set hydrofuge hairs of epicuticle hold a thin film of air indefinitely.

7.8 SUMMARY

Respiratory system is meant for gaseous exchange and oxygen is more readily diffuses than carbon dioxide. This exchange is possible through tracheal system in insects which is a system developed from invagination of the integument. Two diaphragm divides whole thoraco-abdominal cavity into three compartments pericardial, perivisceral and perineural cavities. Insect respiration is specialized system without lungs by a complicated system of

internal tubes and sacs through which gases either diffuse in and out of the body. Due to the absence of RBCs in the haemolyph, oxygen is directly delivered to tissues that need oxygen and carbon dioxide is eliminated through their cells. Usually, spiracles are located on the anterior margin of the mesothorax and metathorax, and on each of the eight or less abdominal segments. Numbers of spiracles vary from 1 to 10 pairs on which basis the insect is said to be holopneustic, oligopneustic, apneustic. The oxygen passes from the tracheae to the tracheoles and lastly to the end cell.

The major tracheae are thickened spirally by taenidia that prevent it from collapsing and often swell into air sacs. There are several types of spiracles, which are closed and opened by valves. The closures of spiracles are essential from losing moisture from the body. There are some aquatic insects have a closed tracheal system, for example, in Odonata, Tricoptera, Ephemeroptera, which have tracheal gills for respiration and having no functional spiracles. The tracheal system may be open or close and number of spiracles may vary from species to species. Aquatic and endoparasitic insects have modification to adapt their environment.

7.9 TERMINAL QUESTIONS AND ANSWERS

Short Answer Type Questions

1. Differentiate between open and closed tracheal system?
2. Draw labeled diagram of tracheal system?
3. What makes insect to respire in water?
4. Write the types of spiracles on the basis of their number?
5. Write a short note on respiratory pigments?

6. Define hemolymph and haemocyte?

Long Answer Type Questions

- Explain different organs of respiration?
- Write down in brief adaptation of endoparasitic and aquatic insect?
- What is the mechanism of respiration?
- Write the composition and function of hemolymph?

UNIT 8: NERVOUS SYSTEM

CONTENTS

8.1 Objectives

8.2 Introduction

8.3 Generalized plan of Nervous System in Insects

8.4 Modifications of Nervous System in Terrestrial and Aquatic Insects

8.5 Summary

8.6 Terminal Questions and Answers

8.1 OBJECTIVES

After studying this module, you shall be able to learn and understand:

i. Basic concept of Nervous system of Insects
ii. Types of Nervous systems in insects
iii. Transmission of nerve impulse in insects
iv. Modifications of Nervous System in Terrestrial and Aquatic Insects

8.2 INTRODUCTION

In the previous unit, we studied the elimination of nitrogenous waste product in insects, through excretory system. This was done by main excretory organ, viz. Malpighian tubules, fat cells, nephrocytes, uricose gland and cuticle.In the current unit, we will study about nervous system in insects.The nervous system is a complex and extended connection between *the sense organs* that respond to numerous internal and external stimuli, and *the effector organs*, like muscles, luminous structure, *etc*. that respond to the stimuli by showing coordinated behavioural changes. The nervous system is made of ramifying *neuroglial cells*, which are supportive and nutritive, along with highly specialized numerous *neurons* that are responsible for rapidly generating and conduct electrochemical nerve impulses. Furthermore, this system contains some nerve cells, which are secretary in nature. The nerve cells are generally found grouped in bundles. Hence, a **nerve** is a pack of axons or dendrites, which functions in the same body part. A **ganglion** is a compacted cluster of interconnected neurons, which process sensory signals and control motor outputs.

8.2.1 NEURONS

The nervous system of insects largely contains an intricate network of specialized cells, which are known as ***neurons,*** which may be considered as an "*information highway*" inside the body. Approximately 10^5 to 10^6 neurons are located in the central nervous system of an insect. Generally, a neuron is comprised of a cell body known as **perikaryon** (or perikaryal when plural) along with one or more long nerve fiber(s) known as the axon. Sometimes, a branch comes out of an axon, which is known as collateral. The cell body is also associated with tiny branch-like processes known as **dendrites**. Similar-looking branching processes rise from the terminal end of the axon, which are known as **terminal arborizations**. These neurons are not directly linked with one another but they communicate either electrically or with the help of special molecules known as **neurotransmitters** or sometimes transmitters. At the terminal end of a neuron, the axon’s terminal arborizations lie in very close association with the dendrites or the axon of another neuron or even end near a muscle known as the **neuromuscular junction**. This junction is a very small distance between dendrites and muscle fibers. The junction between terminal arborizations of axon and dendrites is known as the **synapse**. The neuron that discharges a signal to another is known as a presynaptic neuron, while the posterior neuron that accepts the signal is known as a **postsynaptic neuron**. The neurons generate electrical impulses, which are also called **action potentials** that travel along the cell membrane. This signal transmission is unidirectional and moves away from a nerve cell body along an axon towards another nerve cell body along a dendrite.

The **nerves** are composed of bundles of axons invested in a noncellular neural lamella that is secreted by haemocytes or the underlying glial cells. These nerves then connect the ganglia with other portions of the nervous system. The individual nerve cells are interconnected through special junctions known as synapses. The nerve impulse releasesthe **neurotransmitter,** such asacetylcholine, noradrenaline, dopamine or 5-hydroxytryptamine, which is a chemical messenger, when it reaches the *synapse*. After reaching the synapse, it triggers a new nerve impulse in the dendrite(s) of the connecting neurons.

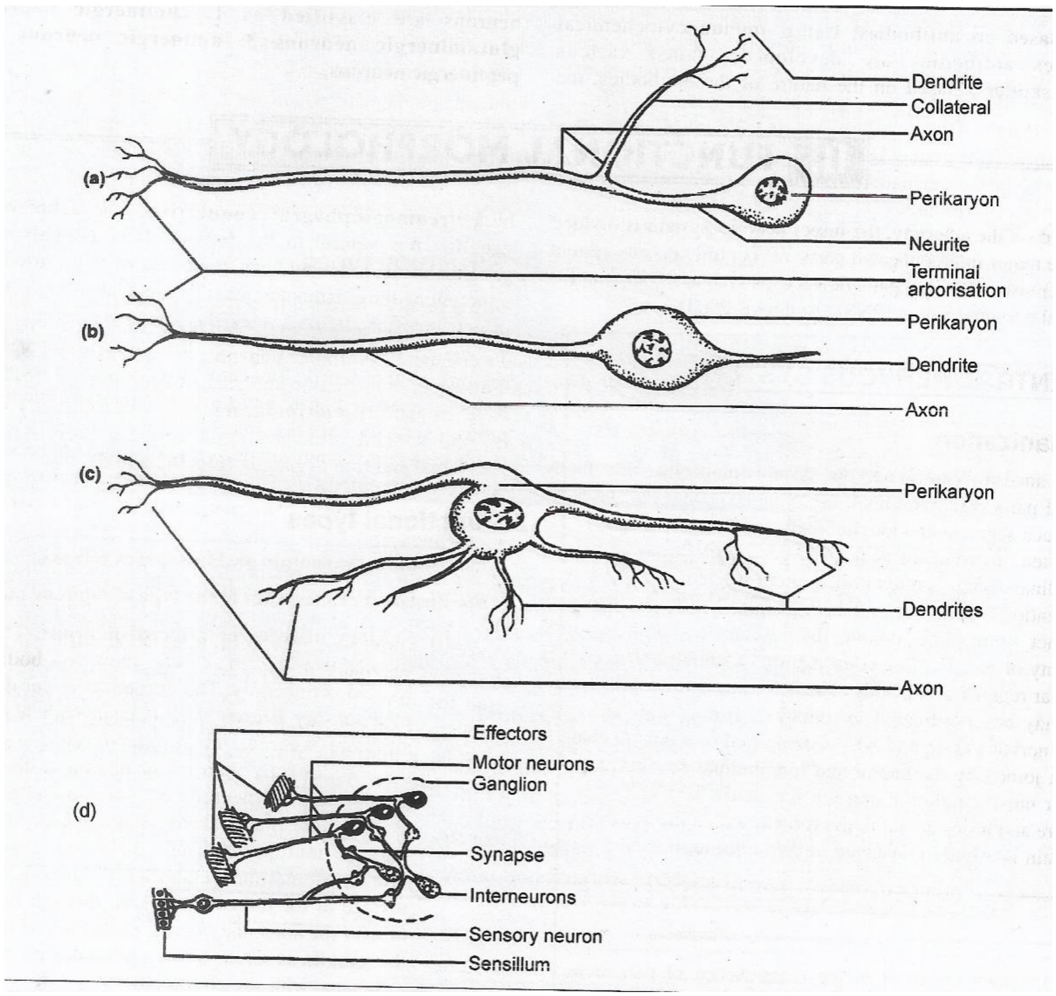


Fig 8.1 Diagrammatic representations of (a) monopolar, (b) bipolar, (c) multipolar neurons, and (d) interactions between sensory, motor and interneurons (Adapted from Ambrose, 2015).

The neurons can be broadly grouped into two types based on their structure and functions. Structurally, the neurons can be classified into three types, *viz*. **(a) monopolar neuron,** which has a single stalk from the perikaryon that connects to the axon and collateral, **(b) bipolar neuron,** which has an axon along with a single branched or unbranched dendrite connected to the perikaryon and **(c) multipolar neuron, which has an axon along with several branched dendrites connected to the cell body perikaryon (Fig 8.1).**

Functionally, there are three kinds of neurons, which are mentioned below as:

(i) Afferent or **sensory neurons**: These types of neurons are bipolar or multipolar cells, which carry the information to the central nervous system. The cell bodies of these neurons are found at the periphery. The dendrites or dorsal processes of these neurons are connected to a sensory structure, while the proximal process is generally linked directly with the motor neuron. Some afferent neurons could be multipolar with their branched distal process. A few multipolar neurons are even associated with stretch receptors.

(ii) Efferent or **Motor neurons**. These are unipolar cells that conduct the information or signals away from the central nervous system and stimulate responses in muscles and glands. Their cell bodies do not have dendrites and are found on the periphery of a ganglion. The motor nerve, which activates muscles, is formed by the bundles of axons from the cell bodies. The collaterals branch of each neuron moves inside the neuropile, while terminal arborizations get connected to the sensory neurons or association neurons. Motor neurons are comparatively smaller in numbers in each ganglion and correspond with a relatively lesser number of muscle units in insects.

(iii) Interneurons or **Internuncial** or **Association neurons**: These are unipolar cells, which usually comprise numerous collaterals and/or axons, which conduct signals or information within the central nervous system. Cell bodies of these neurons are found in the periphery of a ganglion and they synapse with one or many neurons, which may be sensory, motor, or other interneurons. Usually, interneurons are sandwiched or interpolated between sensory and motor neurons. Mostly, the neurons found in the central nervous system as interneurons. Numerous interneurons are limited to the individual ganglion, however, intraganglionic interneurons are also found in other ganglia. For example, about 1500 intraganglionic interneurons are found in mesothoracic ganglion of cockroach, *Periplaneta americana* L., as compared to 200 interganglionic interneurons and 300 motor neurons. The intraganglionic neurons can be **spiking neurons** (which are capable of producing action potentials) or **non-spiking neurons** (which can't produce action potentials). Some interneurons are connected to "giant axons", which are about 45 μm in diameter and run through the entire length of the ventral nerve, as in *P. americana*. The giant axons make a fast conduction system pertaining to alarm reactions and are connected with a wide range of sensory-motor functions in several insect species. For instance, the giant axon in dragonfly naiad (Odonata) is involved in the instant forcible ejection of water from the rectum, and may cause "**jet propulsion**".

The post-synaptic neurons are further grouped, according to their mode of action, into (a) **excitatory neurons**, and (b) **inhibitory neurons**. The details of these are mentioned in 8.3.5.

Similarly, on the basis of nature of antibodies, the neurons are further classified into, **(a) cholinergic neurons, (b) glutaminergic neurons, (c) aminergic neurons, and (d) peptidergic neurons**.

8.3 GENERALIZED PLAN FOR NERVOUS SYSTEM IN INSECTS

Based on the anatomy, the nervous system of insects is divided into three components viz. **(i) Central Nervous System**, **(ii) Visceral or Sympathetic Nervous System**, and **(iii) Peripheral Nervous System (Fig 8.2)**. The detailed generalized plan of the nervous system in insects is mentioned below:

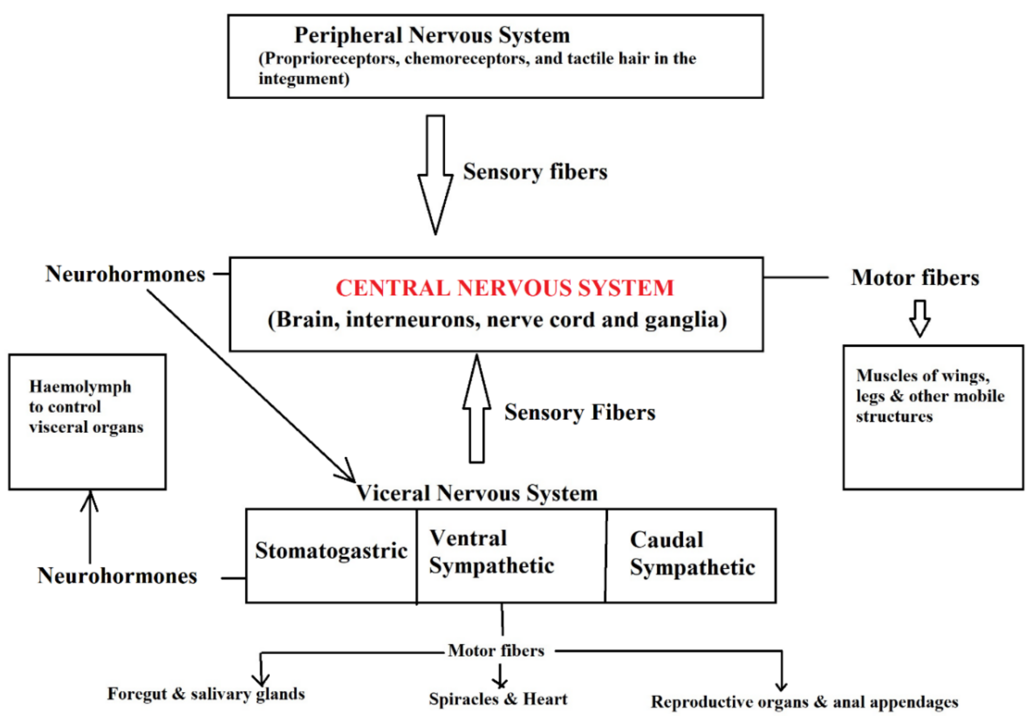


Fig 8.2: Detailed Generalized Plan for the Nervous System in insects.

8.3.2. THE CENTRAL NERVOUS SYSTEM

Like the majority of other arthropods, the central nervous system (CNS) of insects is relatively simple and it comprises a double series of ganglia that are linked to transverse and longitudinal nerve fibres. The transverse nerve fibres are called ***commissures***, which unite the two similar ganglia of a pair. The longitudinal nerve fibres are known as ***connectives***, which connect the preceding and succeeding dissimilar ganglia. Generally, there is a pair of ganglia in each segment, however, these ganglia are so close to each other that the commissures interconnecting them have almost lost their identity. Contrarily, the connectives are distinct and separate throughout the body and can easily be identified. The central nervous system, in general, is more or less ladder-like in appearance. The commissures seem to appear like the rungs of the ladder, while the connectives appear like the rails. In many insect species, the ganglia of adjacent segments may even coalesce and form ***ganglionic centres***. Two such centres are located in the head, while different forms of these ganglionic centres are found in the thoracic and abdominal regions.

The ancestral CNS is made up of segmentally arranged pairs of ganglia, which are connected laterally with each segment, and longitudinally between two segments. These ganglia coalesce to form larger ganglia, and two longitudinal nerves often get united to form a single big nerve. Thus, during the process of cephalization, one to three ganglia fused or coalesced forming a distinct brain. This tends to provide functional autonomy of ganglia, which is the coordination of impulses that tend to involve particular regions of the body. Thus, CNS is comprised of a double chain of ganglia, which are linked together with the help of lateral and longitudinal connectives. The brain is the anterior-most complex ganglionic mass, which is dorsally located to the foregut within the head capsule (Fig 8.3). The brain is generally linked to the suboesophageal ganglion by circumoesophageal connective (the details of this are mentioned below).

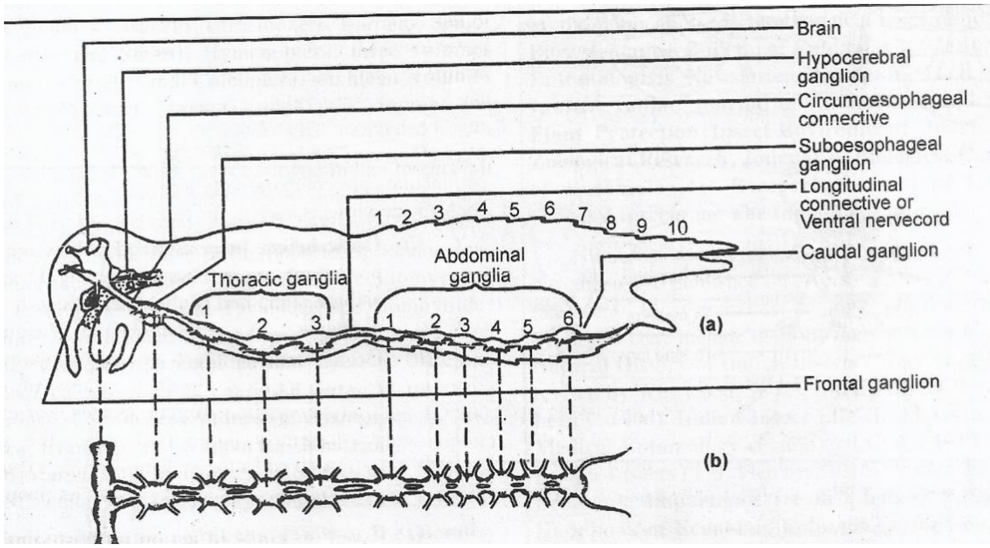


Fig 8.3 Diagrammatic representation showing central nervous system (a) from inside of an insect, and (b) brain and ventral chain ganglia (Adapted from Ambrose, 2015).

The central nervous system of insects is comprised of brain or cerebral ganglion, the suboesophageal ganglion and the ventral nerve cord.

8.3.2.1 The Brain

Insect's brain is located anteriorly to the oesophagus between the apodemes of the tentorium. It consists of a complex of three pairs of fused ganglia that are found dorsally inside the head capsule. It is the head's dorsal ganglionic centre, and its nerve cells are largely association neurons. The brain is divided into three regions, which are known as *protocerebrum*, *deutocerebrum* and *tritocerebrum* (Fig 8.4).

8.3.2.1.1 Protocerebrum: The protocerebrum is the first pair of ganglia and exhibits fused ganglion of *acron* and *pre-antennal system*. It is bilobed and mainly associated with vision, as it innervates ocelli and compound eyes. It is divided into (a) *proto-cerebral lobes*, and (b) *optic lobes*.

(a) *The Proto-cerebral lobes* are fused along the mid-line forming a bilobed ganglion. They are interconnected with a commissural system, which is referred to as the central body. In addition, two smaller commissures, *viz*. i) anterior dorsal commissure (which passes anterior to central body), and ii) posterior dorsal commissure (which lies behind anterior commissure), are found here. Paired *Mushroom bodies or corpora pedunculata* are also formed in the neuropile of proto-cerebral lobes. The mushroom body contains one or two calyces of neuropile comprising calyx cells or *globuli cells*. The calyx continues into the pedunculus of nerve fibre ending deeply into the brain by a complex comprising of alpha, beta and sometimes gamma lobes.

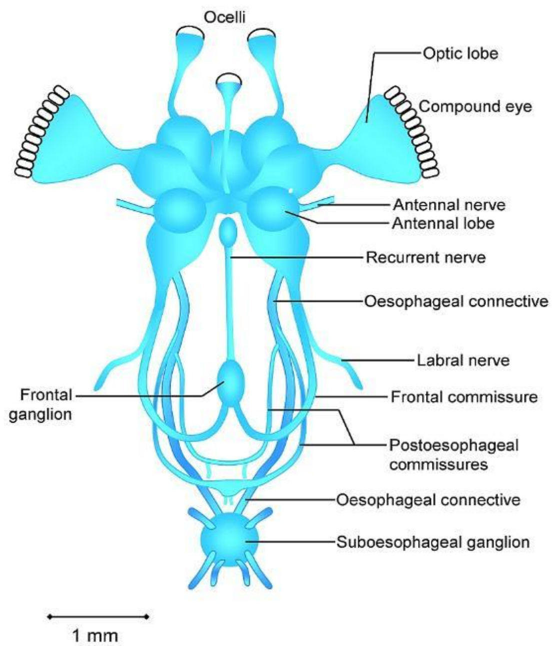


Fig 8.4 Diagrammatic representation of the anterior (frontal) view of the brain of an insect.

(b) *The Optic lobes* form the brain's complex region, which extends laterally from the protocerebrum to the compound eyes. The optic lobes process the sensory inputs received from the compound eyes. Each optic lobe comprised of three neuropile masses or zones of nerve tissues known as the *lamina ganglionaris* (nearest to the eye), the *medulla externa* (middle zone), and the *medulla interna* (inner zone). Each zone includes network of neurons and an array of nervous connections. Short axons arising from the receptor cells of every ommatidium connect with others forming an array of optic cartridges. Electrophysiological studies revealed the occurrence of units in the optic lobes which are essentially responsible for various optic functions, as some of these are involved in movements of small or long parts of the visual fields. Furthermore, some of these units subtend monocular visual fields, while others may cover the entire receptive area of the eyes.

8.3.2.1.2. Deutocerebrum is the second pair of fused ganglia of the antennary segment, which processes the sensory information that antennae receive. It is primarily composed of paired antennal lobes (also known as *olfactory lobes* with nerve connections to antennae) which appear in the form of swellings found on the brain's anteroventral aspect. Four pairs of nerves arise from the deutocerebrum, *viz*. antennary, accessory antennal and tegumentary nerves. The *antennary* nerves are the longest and primarily sensory though they also have motor function. Each antennary nerve has two roots, which are individually derived from the antennal lobe and the dorsal lobe, respectively. The accessory antennal nerves are motor nerves and arise from the antennary lobes. The tegumentary nerves are two slender strands, which arise from the dorsal lobes to the vertex.

8.3.2.1.3. Tritocerebrum is formed by the third pair of ganglia of the head and is largely made of synapses and fibres between the brain, frontal ganglion connectives and suboesophageal ganglion. Tritocerebrum integrates sensory inputs from protocerebrum and deutocerebrum and innervates the labrum. It comprised of a pair of small, widely separated lobes posterior to deutocerebrum, and circumoesophageal connectives arise from it and connect to suboesophageal ganglion. The nerves at the anterior end link it with the frontal ganglion and labrum. In addition, these nerves link the brain with the ventral nerve cord and stomodaeal nervous system, which controls the visceral organs. The tritocerebrum lobes are linked by postoesophageal commissure passing behind the oesophagous. The *para oesophageal connectives* arising from these lobes join brain and suboesophageal ganglion. One of the two *labro-frontal nerves* arising from these lobes passes to the labrum as labral nerve, while the other one forms the root of the frontal ganglion.

8.3.2.2 The Suboesophageal Ganglion is located ventrally in the head capsule (just below the brain and oesophagus) and is formed by the fusion of ganglia of maxillary, mandibular and labial segments (Fig 8.5). The nerves arising from this ganglion innervate the sensory organs and muscles of salivary glands and mouthparts. The movement of the neck and head and neck is controlled by the neurons of this ganglion.

8.3.2.3 The Ventral Nerve Cord –It comprised of various ganglia lying on the floor of the thorax and abdomen. These ganglia are liked into a chain by a pair of connectives. The first three ganglia are known as *thoracic ganglia*, which are found in each thoracic segment and are known to control the locomotor organs. The thoracic ganglion contains 5 or 6 nerves on each side innervating the sensilla and muscles of the thorax and its appendages. The ganglia found in the abdominal region is known as the *abdominal ganglia*. The largest number of these ganglia occurring in larval or adult insects is eight, which is reported in *Machilis*. However, this number greatly varies in most insect species. The last abdominal ganglion is largely compound and derived from the fusion of ganglia of the last four abdominal segments. Nevertheless, the adults of most insect species have further degree of fusion of abdominal ganglia, and in extreme cases even all the ventral ganglia may get fused into one large ganglionic mass, as also reported in *Musca*. Generally, the abdominal ganglia are smaller than thoracic ones and fewer nerves may arise from them. The median nerve in thorax does not run posteriorly beyond the lateral branches, but it usually goes from one ganglion to the next in the abdomen.

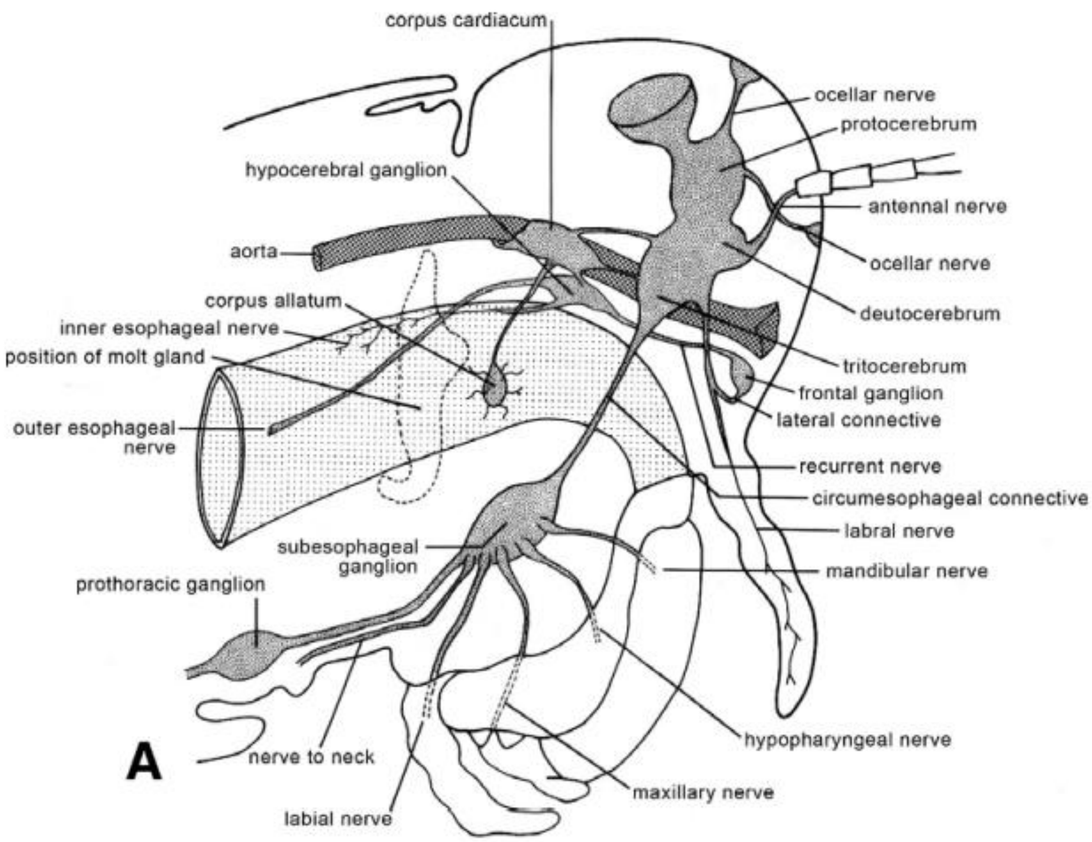


Fig 8.5: Diagrammatic representation showing a lateral view of the Central Nervous System and Stomatogastric Nervous System of an insect.

8.3.3. THE VISCERAL NERVOUS SYSTEM

The Visceral Nervous System is also known as Sympathetic Nervous system. It is divided into (i) oesophageal sympathetic, (ii) ventral sympathetic, and (iii) caudal sympathetic systems.

8.3.3.1. The Oesophageal Sympathetic Nervous System: It is also known as Stomatogastric or Stomodaeal Nervous System, which is connected to the brain and innervates the heart, anterior and middle intestine, and a few other organs. Two frontal nerves arise near the base of the tritocerebrum connecting the brain with a small, triangular, unpaired*frontal ganglion* above the oesophagus. This frontal ganglion innervates pharynx and the muscles related to swallowing. From frontal ganglia arises a median frontal nerve extending forward to the wall of the pharynx, while posteriorly, a *recurrent nerve* runs along the mid-dorsal line of oesophagusbeneath the brain and connects the hypocerebral ganglion that innervates corpora cardiaca, heart, and certain parts of foregut and terminates in the form of *ventricular ganglia*. The insect's nervous system is highly de-centralized and segmental ganglia integrate and control certain important behaviors, like feeding, locomotion, mating, *etc*. rather than the brain. In some cases, the brain can inhibit or stimulate certain activities in segmental ganglia. However, these signals are not so crucial for survival. For instance, a headless insect can survive for days if the neck is sealed preventing any blood loss until it is starved or dehydrated.

8.3.3.2. The Ventral Sympathetic Nervous System: A typical system comprised of a pair of transverse nerves which are associated with every ganglion of the ventral nerve cord. These nerves run to the spiracles of their segments. Insects of a few orders, these nerves are also linked with the *perisympathetic system* comprising of neurohaemal organs releasing products of neurosecretory cells in the ventral ganglion.

8.3.3.3. The Caudal Sympathetic Nervous System: The posterior compound ganglion of the ventral nerve cord gives rise to this system. It innervates the reproductive system along with the posterior part of the gut.

8.3.4. THE PERIPHERAL NERVOUS SYSTEM

The Peripheral Nervous System comprises all the nerves arising from various ganglia of the central and visceral nervous systems. These nerves are made of large number of axons. Within the nerves, the axons are independent and do not branch or form any synapses. The details of neurons, axons, sensory and motor neurons have been discussed earlier in 8.3.1. The dendrites of sensory neurons in the nerves or distal processes are connected with a sensory structure, while the axon usually synapses with neurons within a ganglion of the central nervous system. These nerves are comprised of motor fibers and their cell-bodies reside in the ganglia of CNS, and the nerve fibers terminate on glands, muscles and other effector structures. Peripheral Nervous System's components serve in the form of **"windows"** of the insect. The surface location of sensory structures, like sensilla and other sense organs connect the CNS with the insect's environment. Although sensilla is distributed on the entire body of insects, they are largely aggregated and found on antennae, mouthparts, ovipositor and cerci. These sensilla convert environmental stimuli into some meaningful signals in the form of nerve impulses. The three main concepts of sensory physiology are mentioned below:

1. **Receptor specificity:** A group of different sensilla present on a particular insect organ perceives complex environmental signals. However, a particular sensillum amongst them is highly sensitive and specific to one particular stimulus. For instance, sensilla in the form of chemoreceptors are more sensitive to chemicals as compared to light or sound stimulus.
2. **Receptor transduction:** This is a process in which receptors function as transducers, which are devices that may convert one form of energy into another form. For example, chemical energy is changed into electrical energy when sugar molecules in a solution provide electrical energy to the nerves of insects.
3. **Receptor sensitivity:** Receptors are highly sensitive. There are several factors, like age, sex, genetics, past experiences, hormones, circadian rhythms, *etc*., which can influence, the sensitivity of the receptors.

8.3.5. TRANSMISSION OF NERVE IMPULSE IN INSECTS

Transmission of nerve signals in insects involves three types of processes. First, the incoming signal, which could be mechanical, chemical or visual, is converted into electrical energy, which is also known as transduction. Change in the membrane potential due to an incoming signal is referred to as receptor and in the case of sensory neuron, it is known as generator potential. This change in membrane potential at the synapse is known as post-synaptic potential. Such potentials move passively through neurons; however, they exhibit an exponential decay in amplitude due to the possible leaking of current across the neural membrane. This slowdown of the signal is the reason why the second step is needed. In the second step, the electrical signal is actively transmitted through the axon in the form of the action potential. This covers a large distance in a self-propagating way without a slowdown. However, certain neurons do not produce this action potential. The third step is the usual conversion of an electrical signal into a chemical signal at a synapse to propagate the nerve impulse into the following cell.

8.3.5.1. Action potential:

Action potential spreads with an almost constant amplitude without the slightest decay or a slowdown, which is different from the receptor of post-synaptic potential. When a post-synaptic potential is transformed into an action potential, an analog signal is converted into a digital signal encoded by spike rate and number. Postsynaptic potential or receptor produces current, which gives a small depolarization of membrane in the axon during its passive spread from its origin. This small depolarization is sufficient enough to trigger the opening of voltage-sensitive sodium channels (Fig 8.6.). This leads to a quick positive swing in the charge on inside of membrane, which amounts to 80 – 100 mV, as in cockroach. This is considered as the rising or elevating phase of the action potential. The permeability period of sodium is for a short duration due to the automatic closure of sodium channels and becoming inactivated. There are potassium channels, also known as delayed rectifiers, are also activated by voltage change, which function slower than sodium channels. These potassium channels begin to get opened as the sodium ones are closed. This results in the flowing out of potassium out of nerve fiber and reducing its electrochemical gradient. It makes the inside of the fiber more negatively charged, which is also known as the falling phase of the action potential. The entire duration of the action potential is very small that may last 2 to 3 minutes.

The flow of current is away from the point of depolarization and when it reaches a place of resting membrane, it gives a slight depolarization, which results in a change of its permeability initially to sodium and thereafter to potassium giving rise to the action potential. It is a continuous process resulting in the propagation of action potential along the nerve fiber. However, the refractory condition of the axon can limit the propagation of action potential. The duration at which no action potential is generated can be referred to as the ***absolute refractory period*** and it may last for 2 to 3 minutes. Thereafter action potential can be generated only after receiving a very strong stimulus and as the axon recovers, gradually weaker stimuli can also generate action potential till the level of excitation is normalized. This is known as the ***relative refractory period***, which can be lasted for 10-15 minutes. The rate of propagation of action potential also decreases with time since the reception of stimulus. Initially, the action potentials propagate at a constant rate, however later on the intervals between them increase within a few milliseconds. Such a response is referred to as a ***phasic***response. In numerous nerve fibers, this propagation of action potential is with a constant rate, which is known as the ***tonic*** response. The rate of production of action potential is also referred to as the ***firing rate***.

There are many fibers where firing occurs without any stimulus, unlike action potential that results from the stimulation of receptors. This firing activity is generally achieved by separate classes of ion channel activity instead of those which may produce an action potential. Such additional channels abstain repolarization of the membrane, and maintain the system in a very active state to keep it excited. Big nerve fibers with a diameter 8-50 µm have nerve propagation speed of 3 – 7 m/s, which is lesser in the smaller nerve fibers. As discussed earlier that not each nerve fiber produces action potential. In a few neurons, there occurs a passive spread of post-synaptic sites throughout the cell and can produce changes in membrane potential.

Synaptic Transmission: Action potential when reaches the pre-synaptic terminal get depolarized. This is followed by the opening of the voltage-sensitive channels of calcium in a bid to move calcium ions into the neurons leading to the initiation of complex events that may culminate into the *synaptic transmission*. Calcium ions elevate the probability to fuse the synaptic vesicles with the neuronal membrane, and emit the neurotransmitter into the synaptic cleft. The release of calcium ions is directly proportionate to the frequency of the arrival of action potentials. If the release of calcium ions is greater, then more number of synaptic vesicles released their contents. *Quantum* is the basic quantity of neurotransmitters per vesicle. The release of such transmitter can also occur even in the absence of any electrical activity. The permeability of the post-synaptic membrane is directly affected by the transmitter resulting in the opening of ligand-gated ion channels and activating the second messenger system, *i.e. metabotropic signaling*. In the first case, a post-synaptic change could be a depolarization or hyperpolarization of membrane that depends on the quality of neurotransmitter and the presence of receptors on post-synaptic membrane. Depolarization is generated by opening of cationic channels on the membrane. The inside of membrane reduces its negative charge due to the faster flow of sodium and calcium inside than the flow of potassium ions outside. However, the inward movement of chloride ions increases the negative charge and results in hyperpolarization. Depolarization elevates the probability of generating action potential and is excitatory, while repolarization decreases that probability and is inhibitory. The changes that occurred in this response are known as ***Excitatory postsynaptic potential*** and ***Inhibitory postsynaptic potential***, respectively.

Amongst neurotransmitters in insects, acetylcholine is the major one. Apart from this, other neurotransmitters, viz. serotonin (5-hydroxytryptamine), dopamine, histamine, octapamine and noradrenaline are also identified. Insects have higher concentrations of acetyl choline. Both sensory and interneurons are cholinergic, and the sooner the acetylcholine is released in the synaptic cleft, enzyme acetylcholinesterase initiates the breaking down of this neurotransmitter, which is imperative for the normal functioning of the neuron.

Electrical synapses: An electric synapse is created by a gap junction occurring between two nerve fibers. A direct flow of electric current occurs from pre to post-synaptic cells in the electrical synapse. However, no chemical signals in the form of neurotransmitters occur during the electrical synapse.

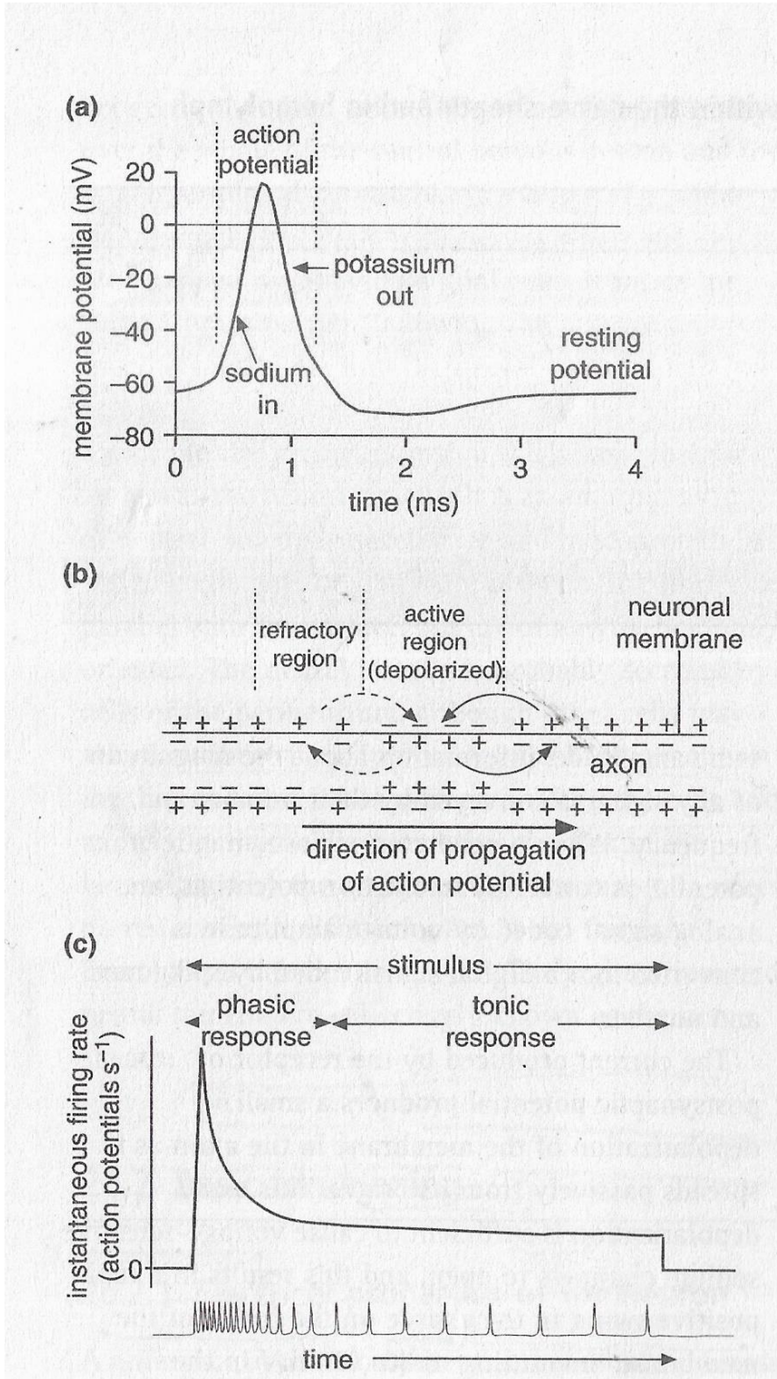


Fig 8.6. Transmission of Action Potential in insects (Adapted from Chapman, 2014).

8.4. MODIFICATIONS OF NERVOUS SYSTEM IN TERRESTRIAL AND AQUATIC INSECTS

The majority of insects are terrestrial and their adult stages are winged or alate and thrive in terrestrial conditions. Aquatic insects, however, include insects that are directly or indirectly associated with an aquatic environment, as one or more of their life stages thrive in water. About 3% of insects are aquatic, which are represented by 13 insect orders, which suggest that a partial aquatic lifestyle is beneficial to a wide array of insects. Usually, aquatic insects are larvae/nymph/pupae of terrestrial adults, which spend some time in terrestrial environments. These insects could be vectors of several diseases, environmental quality biosensors, and are studied to understand aquatic communities and other areas of ecology.

Brain morphology has been studied in several insect orders to give an insight into the modification of their nervous system. Numerous degrees of cerebral development have been found in insects, which are correlated with the intricacies of their sensory equipment or behaviour. For instance, the volume of the brain related to its body is $1/174^{th}$, $1/ 280^{th}$, $1/3290^{th}$, and $1/4200^{th}$ in *Apis*, *Formica*, *Melolontha* and *Dyticus*, respectively. Similarly, the development of optic lobes is proportionate with the eyes, and antennal lobes with the antennae in various insect species. The mushroom bodies in Hymenoptera attained internally, a great size and complexity, which modulate complex elaborate insect behaviour. This is quite evident in the form of insects, after comparing the size of mushroom bodies to the brain, as it is very high in bees and very low in sawflies. Solitary bees attain an intermediate position. Subtle differences in the structure of brains in various morphs of social insects, *viz*. queen, workers and drones are directly associated with the vivid division of labour in the social insects.

If the ventral nerve cord is compared within different groups of insects then the most generalized condition is witnessed in Thysanura, some larvae and a few lower Pterygotes, where certain ganglia, *viz*. suboesophageal-, three thoracic- and eight abdominal – ganglia are separately visible. A few insect orders, *viz*. Mecoptera, Trichoptera and Hymenoptera exhibit slightly more concentration, but the metathoracic ganglion generally fuses with the first three abdominal ones, and the seventh along with the subsequent abdominal ganglia make a compound centre. Similar comparative fusion of ganglia is also conspicuous in other insect orders but at a different level showing the modification in the nervous system.

Certain insects that are secondarily adapted to aquatic environments can sense odours from a varied array of sources. The tracheal system found in nearly all aquatic insects or their respective stages secondarily supports their life in water.

8.5 SUMMARY

The nervous system is a complex connection between the sense organs that respond to numerous internal and external stimuli, and the effector organs, like muscles and luminous structures, which respond to the stimuli by showing coordinated behavioural changes. This system in insects contains an intricate network of specialized cells known as neurons, which may be considered an "information highway" inside the body. Approximately 10^5 to 10^6 neurons are located in the central nervous system of an insect. These neurons are not directly linked with one another but they communicate either electrically or with the help of special molecules known as neurotransmitters or sometimes transmitters. The junction between two neurons is known as the synapse. The neuron that discharges a signal to another is known as a presynaptic neuron, while the posterior neuron that accepts the signal is known as a postsynaptic neuron. The neurons generate electrical impulses known as action potentials that travel along the cell membrane. On the basis of anatomy, the nervous system of insects is divided into three components, viz. (i) Central Nervous System, (ii) Visceral Nervous System, and (iii) Peripheral Nervous System. The Central nervous system (CNS) is simpler and comprises of a double series of ganglia that are linked to transverse and longitudinal nerve fibres. It is also comprised of brain or cerebral ganglion, the suboesophageal ganglion and the ventral nerve cord. The Visceral Nervous System, also known as the Sympathetic Nervous system, is classified into (i) oesophageal sympathetic, (ii) ventral sympathetic, and (iii) caudal sympathetic systems. The Peripheral Nervous System comprised of all the nerves arising from various ganglia of central and visceral nervous systems. These nerves are made of a large number of axons. Within the nerves, the axons are independent and do not branch or form any synapses. Transmission of nerve signals in insects involves three types of processes. The incoming signal, which could be mechanical, chemical or visual, is converted into electrical energy, which is also known as transduction. Action potential spreads with an almost constant amplitude without the slightest decay or a slowdown, which different from receptor of post-synaptic potential. Action potential when reaches the pre-synaptic terminal get depolarized. This is followed by the opening of the voltage sensitive channels of calcium in a bid to move calcium ions into the neurons leading to the initiation of complex events that may culminate into the *synaptic transmission*. A direct flow of electric current occurs from pre to post-synaptic cells in the electrical synapse. The majority of insects are terrestrial and their adult stages are winged or alate and thrive in terrestrial conditions. Aquatic insects include those insects that are directly or indirectly associated with an aquatic environment, as one or more of their life stages thrive in water. Usually, aquatic insects are larvae/nymph/pupae of terrestrial adults, which spend some time in terrestrial environments. Numerous degrees of cerebral development have been found in insects, which are correlated with the intricacies of their sensory equipment or behaviour. Finally, a few insects that are secondarily adapted to aquatic environments can easily sense odours from a varied array of sources.

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8.7 TERMINAL QUESTIONS AND ANSWERS

Question No. 1 Give an account of central nervous system in insects.

Question No. 2: Discuss the peripheral nervous system in insects.

Question No. 3: Describe the transmission of nerve impulse in insects.

Question No. 4: Give an account of autonomous nervous system in insects.

Question No. 5: Give an account of different modification in nervous system of terrestrial and aquatic insects.

Question No. 6: Discuss the synaptic nerve transmission in insects.

UNIT 9: SENSORY, VOCAL AND AUDITORY AND VISUAL ORGANS

CONTENTS

9.1 Objectives

9.2 Introduction

9.3 Structure and functions of different types of Sensory Organs

9.4 Structure and functions of Visual Organs

9.5 Sound producing Organs

9.6 Light Producing Organs: Mechanism, Control and Significance

9.7 Chemoreceptor and Mechanoreceptor: Functions and physiology

9.8 Summary

9.9 Terminal Questions and Answers

9.1 OBJECTIVES

After studying this module, you shall be able to learn and understand:

i. Structure and functions of various sensory organs.
ii. Structure and functions of visual organs.
iii. Sound-producing Organs
iv. Mechanism, control and significance of light-producing organs.
v. Functions and physiology of chemoreceptors and mechanoreceptors.

9.2 INTRODUCTION

In the previous unit, we studied about the nervous system in insects, which is a complex connection between the sense organs that respond to numerous internal and external stimuli, and the effector organs, like muscles and luminous structures, which respond to the stimuli by showing coordinated behavioural changes. This system in insects contains an intricate network of specialized cells known as neurons, which may be considered an "information highway" inside the body. In the current unit, we will discuss sensory organs or receptors, which are those structures where the energy of stimulus that arises externally or inside the insect is transformed in the form of nerve impulse that culminates in the change of behaviour in insect. The fundamental function of the receptors is to receive the stimulus from the external medium and transfer them to effector organs, like muscles and glands. The details of sensory organs and their functions are mentioned below:

9.3 STRUCTURE AND FUNCTIONS OF DIFFERENT TYPES OF SENSORY ORGANS

Sensilla are the organs associated with sensory perception and develop from epidermal cells. The different types of sense organs are:

1. Mechanoreceptors: Insects of this group have processes involving mechanical stimulus. This portion is discussed in detail in 9.7.2.

2. Auditory receptors: Sound is another important stimulus, which is perceived by many insects by their sound receiving organs or auditory receptors. The perception of sound informs the insects regarding mate search, food availability, danger, and other members of the species. The sound is perceived by various organs, which are mentioned below:

(a) Tympanic organ: Also known as tympanal organ is specially adapted for hearing. It consists of a thin membrane or integumental area known as tympanum, which is stretched across a frame supported by an air sac along with the sensory neurons (Fig. 9.1). Sound tends to vibrate the membrane, while chordotonal organs sensed these vibrations. Various tympanic organs in various insect species are found on the thorax, wing's base, the abdomen, and the legs. The tympanal organs are exceedingly evolved in Lepidoptera, particularly in moths, which help them to decipher the echolocation calls of bats. The tympanic organs are located on the tibiae of forelegs of crickets and long-horn grasshoppers. These are located on both sides of abdominal segments of short-horn grasshoppers. These are found on the metathorax and abdomen of noctuid moths and pyralid moths, respectively. The structures of tympanic organs seem to evolve consistently, which also helps determine the taxonomy of the insect species. In short-horn grasshoppers, the tympanic organ is encircled by cuticular rings. The tympanic organ is attached to Muller's organ (which is comprised of numerous scolopophores in the form of swelling), which is linked to metathoracic ganglion *via* auditory nerve.

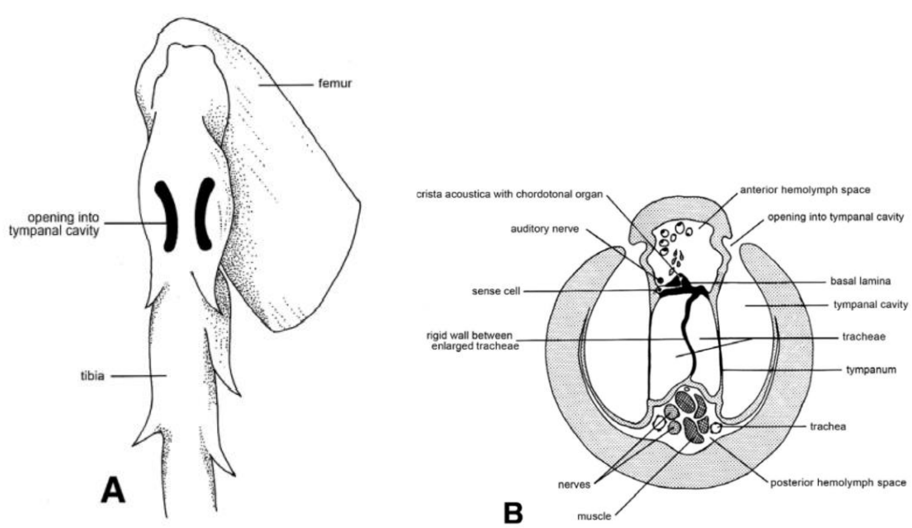

Fig. 9.1: Diagrammatic representation of (A) Surface view of tibial tympanal organ, and (B) Transverse section through tympanal organ of Decticus.

(b) Subgenual organs: These are a cluster of 10-40 scolopidia found in the basal part of tibia. These differ considerably in various insect species, and are highly well-developed in ants, moths, beetles and true flies, while poorly developed in bugs. The subgenual organs are primarily associated with the perception of vibration. The ultrasound vibration is perceived by hawkmoths with the help of structure connected to the mouthparts. Here, the second palpal segment is bulbous and is comprised of an air sac. The medial region of this segment, which is bulbous, touches the pilifer (a tiny appendage associated with the labrum) of the distal lobe. Thus, the ultrasonic vibrations to pilifer that contains sensory transducer *via* palps. In some insects, like cockroaches, sensilla trichoidea located on the cerci is sensitive to perceive airborne sounds.

(c) *Johnston's organ:* Adults and larvae of numerous insects possess a complex chordotonal organ called Johnston's organ located within pedicel, which is the second antennal segment that can sense the movements of antennal flagellum (Fig. 9.2.). It is sensory to sound reception in some species of mosquitoes and midges.

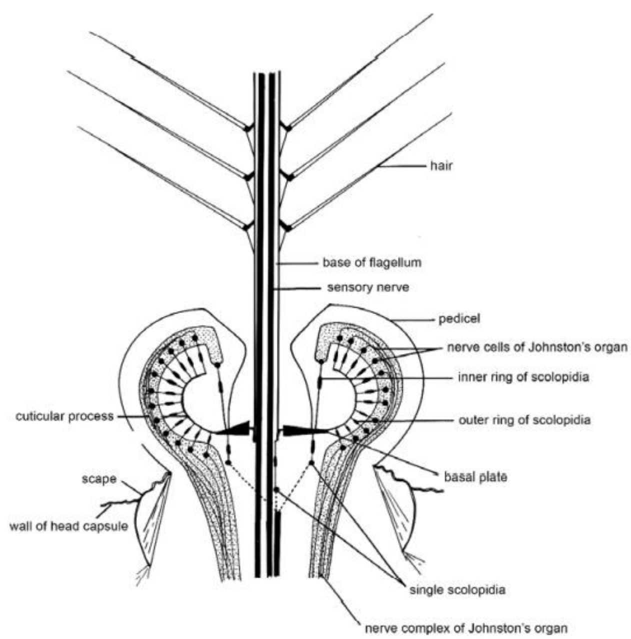

Fig. 9.2. Diagrammatic representation of Johnston Organ

3. Chemoreceptors: These are the receptors, which are associated with perception of chemicals related to smell and taste. It is discussed in detail in 9.7.1.

4. Thermoreceptors: These receptors perceive heat in the form of conduction, convection or radiation showing behavioural changes. A few insects exhibit responses to the radiant heat only, for instance, *Schistocerca gregaria*, which shows a postural response against the sun's radiation. Some poikilothermic insects are sensitive to temperature changes. Blood sucking insects, such as, bed bugs can locate human hosts by perceiving the body heat or temperature gradient of the latter. The temperature receptors are located on the maxillary palps, antennae and tarsi of numerous insect species. Even cold-receptors are found in many insect species. Seemingly, sensilla styloconica is highly sensitive to the decline in temperature regimes.

5. Humidity receptors: Numerous insects can respond to the differences in relative humidity. A few insects can orientate themselves after perceiving water vapour from a distant source. These insects usually prefer a neutral zone and tend to refrain from high or low humidities. A change in feeding behaviour can be seen in *Stomoxyscalcitrans* with an increase in relative humidity. Sensilla basiconica, trichoid or placoid seem to be involved in the reception of humidity.

6. Photo receptors. Insect responses to the light stimulus by (i) Compound eyes, (ii) Dermal receptors, (iii) Dorsal ocelli, and iv) Lateral ocelli or stemmata. Generally, adults are comprised of compound eyes and/ or dorsal ocelli. Certain endopterygote larvae possess lateral ocelli. Insect species living in the dark caves or the absence of light might have degenerated photoreceptors. The details of the photoreceptors in terms of structure and functions of visual organs are mentioned below in the next heading:

9.4 STRUCTURE AND FUNCTIONS OF VISUAL ORGANS

(i) Compound Eyes:In most insect species, a pair of compound eyes are the primary visual organs. These compound eyes are found in approximately all the adults along with the immature stages of insects belonging to ametabolous and hemimetabolous orders. The compound eyes are comprised of numerous individual units called *ommatidium* (plural ommatidia), which are demarcated externally by a hexagonal area known as *facet*. O**mmatidia** are the functional and structural units of vision, and each of this unit is covered by a circle of light-absorbing pigmented cells. The ommatidia in numbers may range from less than six in some worker ants to more than 25,000 in some dragonflies. Each ommatidium is externally marked by corneal lens. A compound eye has two parts, viz. (i) optic part and (ii) sensory part. An optic part consists of a cuticular lens known as corneal lens, which is secreted by corneagenous cells along with a crystalline cone (secreted by a pair of semper cells) enclosed with primary pigment cells. The optic part is meant to gather light. The lens and crystalline cone collectively constitute a dioptric apparatus, which refracts the incoming light into a receptor region that contains visual pigment. The sensory part comprises 6 to 10 visual cells known as retinular cells, which are covered by secondary pigment cells that cumulatively secrete a light sensitive rod in the middle known as *rhabdom*, which consists of light sensitive pigments known as *rhodopsin*. These pigments can absorb incident light of certain wavelengths and can generate photochemical process-driven nerve impulses.

Mostly, the diurnal insects possess pigment cells around each ommatidium, which may limit a facet's field by absorbing light that penetrates through cornea. Each facet may point toward a different portion of a visual field. These facets may provide a **mosaic-like** impression of the outer environment. However, the pigment cells of nocturnal and crepuscular insects do not fully isolate each facet. Light stimulates their ommatidia from larger fields of view, which renders a brighter but less distinct mosaic image.

The visual acuity of insects is comparatively weaker than that of higher vertebrates, as the former cannot form a true and focused image of the outer world. Nevertheless, their propensity to sense movement by tracking objects from each ommatidium is far superior than other higher animals. Temporal resolution of flicker in some bees and flies can be as high as 200 images per second, as compared to about 30 images per second in humans. Majority of insects can differentiate between polarized and unpolarized light, which helps them to locate the sun's position in the sky regardless of the overcast conditions. Insects possess a series of spectral sensitivity that is skewed toward shorter wavelengths, *i.e.* towards higher frequencies, which enable them to see ultraviolet light that humans can't access. Contrarily, insects fail to detect high wavelengths towards red region of the spectrum, which humans can see.

There are two types of "simple eyes", which are found in insects, viz. **dorsal ocelli** and **lateral ocelli (also known as stemmata)**. These two ocelli, however have structural similarities and are considered to have different phylogenetic and embryological origins.

Dorsal ocelli: Adults and immature stages (nymphs) of numerous hemimetabolous insect species have dorsal ocelli. These ocelli are not found in insect species that do not have compound eyes and are not considered to be independent visual organs. They look like two or three small, convex shaped swellings or protuberances on the facial or dorsal head regions (Fig. 9.3). Generally, three dorsal ocelli are found on the frons and vertex of head. In some species, *e.g.*

Blattaria, these ocelli are absent or look like a pair of reduced light sensitive fenestrae. They possess a single corneal lens, which covers an array of many dozen rhabdom-like sensory rods, and are hence quite different from the compound eyes. ***The cornea*** is generally a thickened and transparent portion of cuticle that externally surmounts ocellus to form a lens. ***The corneagen layer*** comprises modified epithelial cells, which are colorless, transparent and can secrete lens. ***The retina*** usually comprises 500-1000 primary sense cells forming a cup and can be arranged into groups of 2 – 5 *retinulae* or cells. Dorsal ocelli do not form any image or perceive any objects in the environment but they can sense a wide range of wavelengths, respond to polarized light, and changes in the intensity of light. Their function is still unknown; however, they seemingly act as an "iris mechanism", *i.e.* they can adjust the sensitivity of the compound eyes to various levels of light intensity.

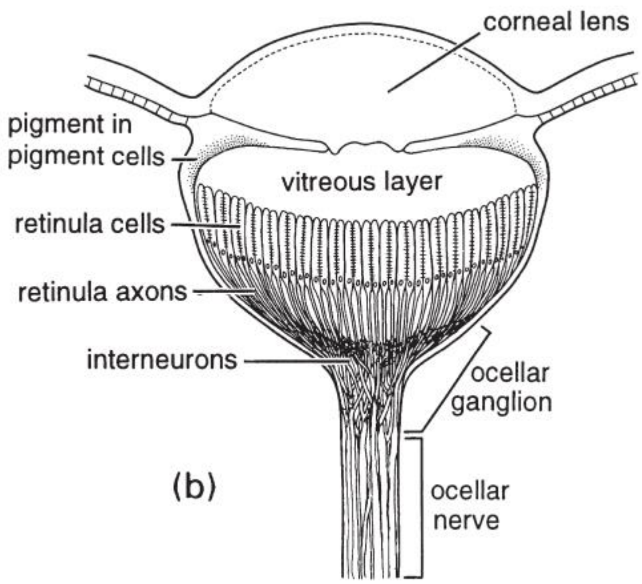

Fig. 9. 3: Diagrammatic representation of a light-adapted median ocellus of an insect.

Lateral ocelli: The lateral ocelli, which are also known as *stemmata*, are considered to be the only visual organs of holometabolous larvae and a few adults of order Collembola, Siphonaptera, and Strepsiptera. They are found towards the lateral side of the head and may vary from one to six in numbers on each side. They are quite similar in structure to dorsal ocelli but they mostly contain a crystalline cone below the cornea and a few sensory rods (Fig. 9.4). Larvae use these ocelli to detect the intensity of light along with the outlines of close objects, and can even detect the movements of prey or predators.

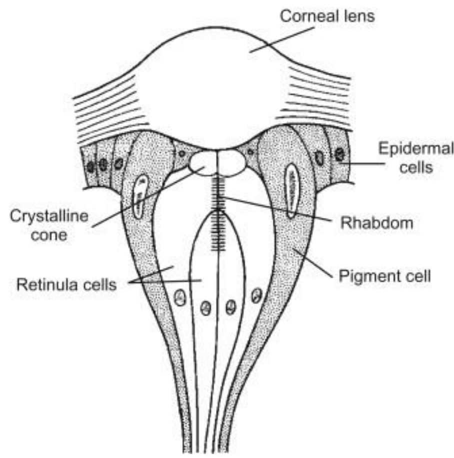

Fig. 9.4: Diagrammatic representation of Lateral ocelli.

Dermal Light Response: Majority of insects seemingly have a light sensitivity on their general body surface. For instance, totally blind cockroaches demonstrate a preference for darker conditions. Similarly, mealworm larvae, *Tenebrio* sp., whose eyes and ocelli have been removed tend to avoid light.

Extra-ocular Photoreception: Some insects can even respond to variations in the intensity of light when all the photoreceptive structures become inoperative. This dermal light sense could be due to the response of each neuron in the brain or ventral nerve cord. Some insects can even perceive infrared radiation, however specific receptors involved in such perception are still unknown.

9.5 SOUND PRODUCING ORGANS

Numerous insects produce sounds of different kinds and intensities from various body parts to communicate with other individuals. The sound producing tendency is sometimes similar in both adult males and females. However, it is strongly developed in certain groups of insects, like grasshoppers and cicadas. The sound is largely produced as calling and courtship songs to attract the mating partner, which is female in most of the cases. It also expresses rivalry between males to show their superiority amongst them. Sound is also produced to warn other individuals as a sign of danger. A single insect species or sometimes an individual can produce a variety of sounds, which have different meanings and functions. The sound is produced by various methods, which are mentioned below:

9.5.1. Sounds produced by tapping body parts against a substratum or external object:

Many insects produce sound by tapping the substratum with their body-parts to communicate with other individuals of their species. The mechanism of producing vibrations, *i.e.* striking the body part against a substrata or clapping the body-parts with each other is known as Percussion. A single tap of a body part on a solid surface generates a complex wave pattern with varied spectral composition and propagation.

In termites, soldiers of *Zootermopsis* generate repeated series of tapping sound by banging their heads up and down, thumping their mandibles on ground and hitting the dorsal part of their heads on the roof of the chambers or galleries. Similar head movements and sound generation have also been observed in workers and larvae. A death watch beetle, *Xestobiumrufovillosum* produces tapping sounds by banging its head on the floor of its burrow, which seems to be sexual call. Some female booklice (Psocoptera) possess a small knob like structure on ventral side of their abdomen, which they bang on the ground to produce sound. Some grasshoppers drum on the ground with its hind tibia. Some termites bang different parts of their bodies against the substratum.

9.5.2. Sounds produced by friction of one body part against the other:

Numerous insects emit sounds by rubbing a body part against the other, and the body part generating the sound is referred to as *stridulating organ* and the process is known as *stridulation*. The stridulation is the generation of vibrations by moving a *scraper or plectrum* (a cuticular ridge) on one body part over a toothed ridge of another, which is also known as roughened a file or a *strigil*. The repetition of contacts of scraper on the teeth of strigil results in the vibration of body parts. This frictional sound is produced by a few insect orders but the members of Orthoptera, Heteroptera, and Coleoptera are the major sound producers.

In order Orthoptera, two main methods of stridulation are identified, which are (i) tegminalstridulation in Grylloidea (crickets) and Tettigonioidea (bush crickets), and (ii) femoro-tegminalstridulation in Acridoidea (grasshoppers). However, mantids produce sound by abdomino- alary stridulations. Many species of Heteroptera stridulate different body parts to produce sound. For instance, the individuals of Pentatomomorpha rub the file present on the ventral surface with a scraper present on the leg. Some species of this group may also rub the file located on their wings against the scraper located at the dorsal surface of the body. Almost all the species of Reduvioidea possess a file between their front coxae (legs) which is rasped by the rostrum's tip. Numerous aquatic heteropterans stridulate under the water using their various body-parts. For example, *Ranatra* possesses a file on its front leg (fore femora) with a scraper on its coxa. *Buenoa* sp. also possesses a similar arrangement of stridulating organ. In these aquatic insects, the air bubble acts as resonator, which is generally carried beneath the surface for the oxygen intake. In certain corixids, this air bubble tends to vibrate due to the movements of head when it the femoral file rubs it. The frictional method of stridulation is also very common in certain homopterans, *e.g.* aphid, *Toxoptera* and some psyllids.

In the beetles' family, Coleoptera numerous body parts are stridulating organs and the most common body parts are elytra or forewings. For example, striated ridge along the edge of the elytra in *Oxycheila* sp. is rubbed by the ridged area of hindleg. Similarly, some coleopteran larvae stridulate with the help of numerous ridges located on the coxa of middle legs with a scarper located on the trochanter on hind leg. In certain larval passalids, hind legs are highly reduced and only function as scraper and are not used for locomotion purposes.

In Lepidoptera, all the developing stages including larvae, pupae and adults can generate sound through stridulation. Lycaenid and riodinid butterflies can produce sound using the file located at the ends of abdominal segments. Pupae of various families like Lymantriidae, Papilionidae, Hesperiidae and Saturnidae stridulate by rubbing transverse ridges present on the anterior edges of some abdominal segments against fine tubercles found on posterior edges of the segments anterior to them. Similarly, in Odonata, the *Epiophleha* larva has side ridges areas on abdominal segments 3 to 7, which are rubbed by ridged inner surface of femur of hind legs to generate sound. In ants, the sound is generated by the movement of scraper on petiole against the striation found at the base of gaster. Finally, in dipterans, the stridulation is very widespread. For instance, the cubito-anal area of wings of *Dacustryoni* vibrates dorsoventrally across the twin rows of 20-24 bristles found on third abdominal segment to produce sound.

9.5.3. Sounds produced by vibrating wings on the thoracic wall:

Numerous insects produce a humming or buzzing sound when they fly. The frequency of the sound in the form of emitted note may appear similar to that of the wing-beat. It is quite prominent in the case of fruitfly, *Drosophila funebris*, where each round of wing movement depicts one sound. In certain dipterans and hymenopterans, apart from the main wing-beat and its harmonics, an additional high frequency sound occurs on every half-cycle of the wing-beat probably due to the vibration of thoracic skeleton. The males of different species of *Drosophila* can produce characteristic courtship songs from the vibrations of wings. These courtship songs are composed of repeated pulses of sound, which helps the females to recognize the courting males.

9.5.4. Sounds produced by vibrating special membrane due to muscular action:

Sounds are generated by vibrating the membrane, which is directly driven by muscles. This kind of sound production is very common in Auchenorrhynchan Homoptera and Heteroptera (Pentatomidae) along with some Lepidoptera (Arctiidae). It is most studied in the male Cicadidae and is one of the most complex sound producing organs in insects. Females either do not have this organ or they possess it rudiments. Cicadas emit the greatest volumes of sound, which make them the noisiest candidates among insects. The sound producing apparatus consists of a pair of tymbals (or shell-like drums) found at the base of abdomen, which vibrate by the action of muscles. Sound is generated as the tymbal muscle contracts, which pulls the tymbal and buckles it inward generating a click sound. When tymbal muscle relaxes, the tymbal gets returned to its usual position because of elasticity and generates a second click. Often, there are large air sacs beneath the membrane that help in the amplification of sound.

9.5.5. Sounds produced by the expulsion or emission of air:

The expulsion of air is a very rare phenomenon in terms of sound production in insects. It is well noted in the death’s head hawk moth, *Acherontia*, which sucks air in and then expels it out through mouth by dilation and contraction of pharynx. The consistent contraction of pharynx along with epipharynx results in the expelling of air and producing a whistle like sound. Usually, two sounds are emitted. First sound is a low note accompanied by vibrations of epipharynx, while the second is a high-pitched whistle due to the free passage of air. The acoustic signals produced by male hissing cockroach, *Gromphadorhina* during male-male competition and courtship is a classic example of sound emitting by the expulsion of air. This sound is generated due to expelling of air through an enlarged fourth abdominal spiracle. The frequency of sound produced may range from 10 kHz to 40 kHz.

9.5.6. Sounds produced as a by-product of some other activity:

Various frequencies and pitch of sounds are produced when insects are cleaning, feeding, or copulating, however little is known about their significance. For instance, sounds generated during flight of an insect seemingly have some significance. The frequency of wingbeat is comparatively constant within a species but it may vary with age, food, sex and temperature.

9.6 LIGHT PRODUCING ORGANS: MECHANISM, CONTROL ND SIGNIFICANCE

Bioluminescence or intrinsic luminescence is the light produced by insects and is well known in a few families of order Coleoptera, *viz*. Lampyridae (fireflies), Phengodidae (railroad worms) and Elateridae (click beetles). A few species of other insect orders, *viz*. *Onychiurusarmatus* (Collembola), *Fulgora lanternaria* (Homoptera) and some larvae of Diptera are known to produce light.

9.6.1. Light producing organs:

The light producing organs can be found in different parts of the body. *Onychiurus*emits light in the form of a glow from the entire body. In beetles, the light producing organs are comparatively compact and are located on the ventral side of the abdomen. A pair of light organs are found at the ventral side of 6th and 7th abdominal segment of male *Photuris* (Coleoptera). In females, these organs are smaller than males and are located only in one segment. The larvae possess a pair of such organs on the eighth segment, however which are lost during metamorphosis into the adult form. Eleven pairs of dorso-lateral light producing organs are found on the thorax and abdomen of the larvae and females of Phengodidae. However, in Fulgora, the light organ is located on the head. The light organ of glow-worm fly, *Arachnocampa* of order Diptera formed from the enlarged ends of Malpighian tubules.

9.6.1.1. Structure of light producing organ

Smith (1963) studied the structure of light organ or lantern in adult *Photuris* and described it in great detail. Each light organ is comprised of numerous large cells known as *photocytes*, which lie just below the epidermis and are supported by a few layers of cells known as *dorsal layer cells*. The light producing organ is lined by a transparent layer of cuticle. The arrangement of photocytes is in the form of cylinders positioning at right angle to the cuticle. Each of these cylinders contains tracheae and nerves. Each trachea gives rise to branches at the right angles, which are further divided into a number of tracheoles when they enter the area of the photocytes and run between photocytes parallel with cuticle. The origin of tracheoles is surrounded by a large tracheal end cell, whose inner membrane, where the tracheoblast is bound, is folded complexly. The nerves that enter the photocytes cylinder terminate as spatulate terminal processes between the tracheoblast and plasma membranes of the end cell, which give rise to tracheoles. In *Pteroptyx* (Coleoptera) and a few insects, nerve endings are found on both tracheal end cells and the photocytes.

Two types of vesicles (large and smaller) are found within the terminal process. The large ones are about 100nm, while the smaller ones are 20-40 nm. The photocytes consist of photocyte granules containing a cavity, which connects with the external cytoplasm *via* a neck. Seemingly, the reactants necessary to produce light are found in these granules. Some small granules are also found both ventrally and dorsally. Mitochondria are also found, which are scarcely distributed except where the cell connects with the end cells and the tracheoles. The dorsal layer cells, forming a reflecting layer behind the light producing organ, are also comprised of granules that are usually regarded as urate granules. These cells efficiently direct the light in the outward direction. Two lanterns in *Photuris* sp. contain about 15000 photocytes, which form about 6000 cylinders, each comprising 80-100 end cells. Organization of lanterns in larval fireflies is simpler and contains the same elements as that of adults. Their tracheal system is diffused with no tracheal end cell.

9.6.1.2. Bio-molecules of Luminescence

The major compounds associated with light production are:

(i). *Luciferase*: It is an enzyme.

(ii). *Luciferin*: It is a low molecular weight compound secreted by photocyte, which could be an aldehyde, a polypeptide or a protein.

(iii). *Luciferin binding protein*: It binds with luciferin.

(iv). *Photoprotein*: It is a protein chromatophore.

(v). *Scintillion*: ATP and Mg^{++}

These compounds vary extensively in their properties from one group of organisms to another and even in their occurrence.

9.6.2. Mechanism of light production

Light is produced in peroxisomes, which are cell organelles where enzymatic oxidation reactions take place. The compound luciferin is oxidized in the presence of enzyme luciferase. The luciferin, however, is first activated by ATP in the presence of luciferase and magnesium ions to produce adenyl luciferin. This gets oxidized by an organic peroxide in the presence of luciferase forming the excited adenyl oxyluciferin, which decays instantly to low energy adenyl oxyluciferin with an emission of light. The energy required for this reaction is directly obtained from the process of oxidation and not from ATP, and it gets released in a single large step. The reaction is highly energy conservative, as about 98% of energy involved is released as light. In addition, the metabolic costs involved in light production in fireflies are very low. It also elevates the metabolic rates by 40% as compared to 60% for walking activity. The low energy adenyl oxylurciferin inhibits further reaction, perhaps because of binding to luciferase pyrophosphate. It is likely that when light producing organ is stimulated by a neuron, the acetylcholine released at the nerve-ending reacts with co-enzyme A and ATP to yield pyrophosphate. This finally diffused to the photocyte granules and triggers light production by eliminating the inhibition of luciferase. During reaction, more pyrophosphate is released in the photocyte, which may further spread through the cell and thereby extending the reaction.

In most insects, such as *Photinus* and *Lampyris*, the light produced is yellow – green, which extends in narrow range of wavelength, *i.e.* 520-650 nm. This range was further restricted to yellow – orange with wavelength ranging between 520- 590 nm in the larvae and adult females of railroad worm, *Phrixothrix*. Similarly, the light emitted by *Arachnocampus* (Diptera) and *Fulgora* (Hemiptera) is blue-green and white, respectively.

9.6.3. Control of light production:

Light is produced from a chemical stimulus. The nerve impulse arrives at nerve ending can lead to the release of acetylcholine, which diffuses out and initiates the reaction of photocytes. So, by obstructing the nerve impulse by any means can stop the light production.

The production of light entirely depends on O_2 supply. So, by regulating the O_2 supply light production can also be regulated and controlled. The light production can also be controlled by Central Nervous System along with certain hormones.

9.6.4. Significance of light production:

In insect, the production of light has functional significance, *i.e.* to lure the mating partner or opposite gender for mating purpose, to attract prey for food, and for the defense. The details of which are mentioned below:

(i)Species recognition: In certain insect species, the light production attracts the individuals of the same species to congregate at a place and it may also indirectly increase the prospects of mating.

(ii) Mating signal: In most of the light producing insects, the emission of light seems to have a sexual significance. The sexual recognition largely depends on species specific signals. The light wavelength is constant within the species however it may vary between the species. The timing of flash and the interval between the two flashes are often characteristic. For instance, constant glow of female *Lampyris* helps to attract the male. The adult fireflies, *Photurispyrolis* come out at dusk and emit a single short flash at regular breaks. Male fireflies usually emit flashes to seek mates and they outnumber the females with the ratio of fifty to one. When males emit flashes within 10-12 feet of the females, the latter climb a blade of grass flashing. The signals are exchanged repeatedly about 5-10 times, which then culminate into mating.

(iii) Predation: Numerous insects produce light to attract prey for predation. An interesting example of light emission to lure the prey is found in the glow-worm fly of New Zealand, *Arachnocampaluminosa*. The female fly lays eggs on the roof of dark caves. After hatching from the eggs, the glow-worm fly larvae hang down from the ceiling by a sticky thread and emit light. This results in the glowing of entire cave during night with this light that ultimately attracts other insect species that will be preyed upon. These insects get trapped and entangled in the sticky threads and ended up as a food for the larvae. These caves, which are inhabited by glow-worm flies are commonly known as "*luminous caves*" and are famous tourist spots in New Zealand. Similarly, the light produced by *Bolitophila* larvae serves as a lure to attract insects on which they feed into webs of glutinous silk threads.

(iv)Defense: Light may also protect the insect and serve as shielding device against predators. It can warn or frighten the predators. The continuous glow of head region in railroad worms when their larvae are walking may suggest a possible illumination function. However, the conditions under which the lateral light producing organs are switched 'on' seemingly suggest a defense function. Sudden light flashes can even repel potential predators. The larvae of railroad worm inhabiting at high densities and confined to small areas may use successive emission of light to scare its enemies or light can also be used to intimate the mated females to oviposit, about overcrowding, and about competition for food sources.

9.7 CHEMORECEPTOR AND MECHANORECEPTOR: FUNCTIONS AND PHYSIOLOGY

9.7.1. Chemoreceptors: These are the receptors, which are associated with perception of chemicals related to smell and taste. The chemical cues are useful to insects in mate-location, mate-recognition, food-perception, alarming for the enemy, identifying individuals of same and different species, *etc*. The chemicals are largely perceived by the sensilla located on the antennae, mouthparts, thorax, legs and other body parts of insects. Certain sensilla responsible for the chemoreception are mentioned below:

(i) Sensilla chaetica: These are the longest sensilla present on the entire antennae and other body parts of insects (Fig. 9.5). They possess longitudinally arranged furrows and are of various sizes in the individuals of same species. This sensillum is primarily mechanoreceptive in function, while in some insects, particularly ladybird beetles, it is also involved in mate-recognition.

(ii) Sensilla Trichoidea: Sensilla trichoidea are the second-longest sensilla found on the antennae and mouthparts of the insects. These sensilla are slender hair-like structures, slightly tapered from base to top. They are primarily associated with thigmo-reception that identifies the food-types and can perceive the finest details of the food. In certain species of ladybird beetles these sensilla are responsible for long distance olfaction and are involved in aggregative behaviour and mass aggregation.

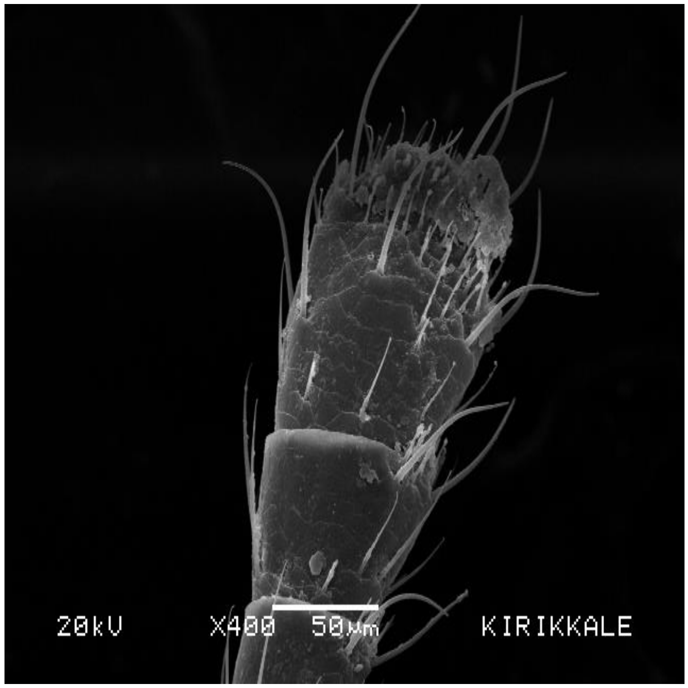

Fig. 9.5. Scanning electron microphotograph showing sensilla chaetica and trichoidea (© Pervez).

(iii) Sensilla Basiconica: These sensilla are stout peg-like structures found mostly on the antennae of the insects. They are gustatory in function and are associated with food detection. They are also involved in long distance chemoreception enabling mate search and recognition. Sensillum basiconica also has thermo- and hygro-sensory-receptive functions along with CO_2 perception.

(iv) Sensilla Campaniformia: This sensillum is a knob-like, dome-shaped structure with a circular depression at the centre. It helps in proprio-reception and also has a gustatory function.

(v) Sensilla Coeloconicum. This sensillum is a single pore-like small aperture consisting of a tiny peg, which is about 8μm in length, embedded in a cavity that is about 20μm in diameter. It is known for hygro- and thermo-reception. It also perceives carbon-dioxide, water vapour, and temperature fluctuations.

(a) Olfactory receptors: Primarily, sensilla basiconica and coeloconica functions as olfactory receptors. They contain numerous pores, which perceive chemicals and transmit them to the nerve endings. A few neurons are linked with these sensilla, which are highly sensitive, exhibiting high degree of specificity and can perceive chemicals at very low concentration in the gaseous state. These olfactory receptors are largely located on the antennae and mouthparts of

insects. Some insects, particularly moths for *e.g.* male silkmoth and gypsy moth can perceive chemical odours, bombykol and gyplure, respectively from very long distances. Even a single molecule of these odours (commonly known as pheromones) is enough to induce an impulse in the receptor cells of male moth.

(b) Gustatory receptors: Sensilla trichoidea, styloconica and basiconica are mainly responsible for gustatory reception in insects. These receptors largely perceive chemicals, which are non-volatile and occurs in the aqueous forms. Thus, these sensilla are also known for contact chemoreception and show responses during feeding stimuli and to reject non-palatable foods. These sensilla are usually located on the maxillary and labial palps along with tarsi.

9.7.2. Mechanoreceptors: Insects of this group have processes involving mechanical stimulus. They possess sense of touch, which include contact with current air, solid objects and water. Few main mechanoreceptors have been identified.

(a) Articulating sensory hairs: The sensory hair or trichoid sensilla (also known as sensillum trichoidea) are specialized structures on antennae, mouthparts, tarsi, cerci, *etc*. Sensillum trichoidea comprises of tormogen cells and trichogen, which simultaneously secrete socket and the hair (seta), respectively. These cells are highly touch sensitive. These sensilla are grouped into structures, which are also referred to as 'hair plates' or 'bristle fields', and are responsible for proprio-reception.

(b) *Sensilla campaniformia*: They are also known as campaniform sensilla. Each sensillum consists of a rod like terminal structure embedded into a small dome-shape structure with a relatively thinner cuticle surrounding it. These are largely sensitive to pressure and found on the antennae, leg joints and wing bases.

(c) *Chordotonal Organs (Scoloparia):* They are the specialized sensory organs which receive vibrations and are interoceptors that are located at both the ends of body wall. These complex structures are comprised of numerous specialized sensilla, *viz*. scolopophores or scolopidia. Each scolopidia is comprised of scolopale cell, cap cell, and dendrite. Chordotonal organ on the proximal tibia of the leg can sense the substrate vibration.

(d) *Multipolar stretch receptors:* These receptors are comprised of multipolar Type II neuron, which is associated with muscles or connective tissues.

9.8 SUMMARY

Insects are gifted with various sensory organs pertaining to vision, sound, touch, smell and producing light. It’s hearing aid is due to various organs found in the insects, *viz*. Tympanic organ, subgenual organs and Johnston's organ. Insect responses to the light stimulus by (i) Compound eyes, (ii) Dermal receptors, (iii) Dorsal ocelli, and iv) Lateral ocelli or stemmata. Usually, the adult insects possess compound eyes and/ or dorsal ocelli. In most species, a pair of compound eyes are primary visual organs, which are comprised of numerous units called *ommatidium* (plural ommatidia). In addition, two types of “simple eyes” are found, viz. dorsal ocelli and lateral ocelli (also known as stemmata). Many insects produce sounds of different kinds and intensities from various body parts to communicate with other individuals. Such sounds can be produced by (i) friction of one body part against the other, (ii) tapping body parts against a substratum or external object, (iii) vibrating wings on the thoracic wall, (iv) vibrating special membrane due to muscular action, (v) the expulsion or emission of air, and (vi) sounds are also produced as a by-product of some other activities. Bioluminescence or intrinsic luminescence is the light produced by insects is well known in a few insect families. Light producing organs are found in various parts of insect body, which are mainly found in its abdominal segments. The major compounds associated with light production are Luciferase, Luciferin, Luciferin binding protein, Photoprotein and Scintillion. Insects also possess chemoreceptors, which are associated with perception of chemicals related to smell and taste. These chemical cues help insects in mate-location, mate-recognition, food-perception, alarming for the enemy, identifying individuals of same and different species, *etc*. The chemicals are perceived by the sensilla located on the antennae, mouthparts, thorax, legs and other body parts of insects. These sensilla are, (i) sensilla chaetica, (ii) sensilla trichoidea, (iii) sensilla basiconica, (iv) sensilla campaniformia, and (v) sensilla coeloconicum. the mechanoreceptors include, articulating sensory hairs, sensilla campaniformia, chordotonal organs (scoloparia), and multipolar stretch receptors. These sensory organs help insects to smell and taste.

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9.10 TERMINAL QUESTIONS AND ANSWERS

Question No.1 Describe structure and functions of different types of sensory organs in insects?

Question No.2 Give an account of structure and functions of visual organs found in insects?

Question No.3 Discuss various sound producing organs of insects?

Question No.4 Explain the mechanism, control and significance of Light producing organs in insects?

Question No.5 Give an account of different types of mechanoreceptors found in insects?

Question No.6 Explain bioluminescence in insects?

Question No.7 Explain various ways by which sound is produced by the insects?

UNIT 10: REPRODUCTIVE SYSTEM

CONTENTS

10.1 Objectives

10.2 Introduction

10.3 Structure and Modification of Male and Female Reproductive Organs

10.4 Spermatogenesis and Oogenesis

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10.10 Terminal Questions and Answers

6.1 OBJECTIVES

After studying this module, you shall be able to learn and understand:

i. Structure and modification of male and female reproductive organs of insects.

ii. Mechanism of spermatogenesis and oogenesis in insects.

iii. Events related to mating in insects.

iv. Processes and mode of insemination in insects.

v. Mechanism and control of oviposition in insects.

vi. Special modes of reproduction in insects.

6.2 INTRODUCTION

In the previous unit, we studied about various sensory organs pertaining to vision, sound, touch, smell and producing light in insects. In the current unit, we will discuss the reproductive system of the insects. Insects have the high reproductive capacity and a single female insect produces a large number of offspring. This is the reason why insects are the most successful group of living organisms on this planet. Many interesting aspects of evolution can be displayed from the reproduction of insects, such as sexual selection, sexual conflicts, cryptic mate-choice and male-male competition, *etc*. Certain behavioural aspects, such as courtship behaviour and calling behaviour are also evident in this group. Insects are also gifted with a unique sense of odour-reception and there are certain moths, like gypsy moths who can sense the presence of their mating partners from a distance of 12 km by perceiving their odours. Generally, male and female insects differ in sexes and dioecious condition prevails. Sexual dimorphism, *i.e.* male and female insects have distinguishable morphological features, which help in the external identification of the two sexes. The details of male and female reproductive systems, spermatogenesis, oogenesis, insemination, mating, oviposition and different special modes of reproduction have been mentioned below:

10.3 STRUCTURE AND MODIFICATION OF MALE AND FEMALE REPRODUCTIVE ORGANS

The sexes in adult male and female insects are mostly separate. There exists sexual dimorphism, as males morphologically differ from the females. In addition, there exists other types of sexual forms, viz. *Gynandromorphs* (Sexual mosaic), which are individuals possessing secondary sexual characters of both the adult forms, e.g. mutant *Drosophila*, and hermaphrodite, where both male and female sex-organs are found in one organism. *e.g. Iceryapurchasi* (cottony cushion scale).

10.3.1. MALE REPRODUCTIVE SYSTEM: The male reproductive system is mainly associated with production and storage of sperm along with their transportation to the female genital tract. Male reproductive system consists of paired testes containing a series of testicular follicles, where the sperm are produced (Fig. 10.1). The details of which are mentioned below:

(i) Testis. The testes usually lie above or below the gut in the abdominal region. Generally, each of the testis consists of a series of tubes or testicular follicles, which range from one in number in beetles (Adephaga) to even more than one hundred in grasshoppers (Acrididae). Sometimes, the testicular follicles are incompletely detached from each other, as observed in Lepidoptera, or they may be grouped into separate lobes, as found in Cerambicidae.

(ii)Vas deferens and seminal vesicle. Each testicular follicle gives rise to a very fine vas efferens, which further connect to the vas deferens (or vasa deferentia in plural). This vas deferens is a tube containing a thick bounding epithelium known as basal lamina along with a layer of circular muscle outside it. The vas deferens runs backwards leading into the distal end of ejaculatory duct. The seminal vesicles store sperm prior to their transfer to the females. In numerous insects, these vesicles are dilations of vas deferens. However, in some insects, like hymenopteran, these vesicles are just dilations of the ejaculatory duct.

(iii) Ejaculatory duct. Vasa deferentia connect to a median duct known as the ejaculatory duct that generally opens towards posterior end into the membrane between 9th and 10th abdominal segments. Some insects, for example, Ephemeroptera do not have any ejaculatory duct. Hence, vasa deferentia, directly, leads to the paired genital openings. Some insects, like Dermaptera, contain a pair of ejaculatory ducts, while one of the ejaculatory ducts remains vestigial in some insects, *viz. Forficula*. In some insects, parts of the epithelial wall of the ejaculatory duct can be glandular, which contributes reproductive proteins to the ejaculate. The circular lumen of the lower part of ejaculatory duct leads to ejaculatory sac and spermatophore sac.

(iv) The Aedeagus or Male Genitalia. The terminal end of the ejaculatory duct gets enclosed into a finger-like evagination of the ventral body-wall forming aedeagus or a male intromittent organ. This aedeagus differs in morphology in various insect species within the family and is considered a characteristic feature for the identification of species.

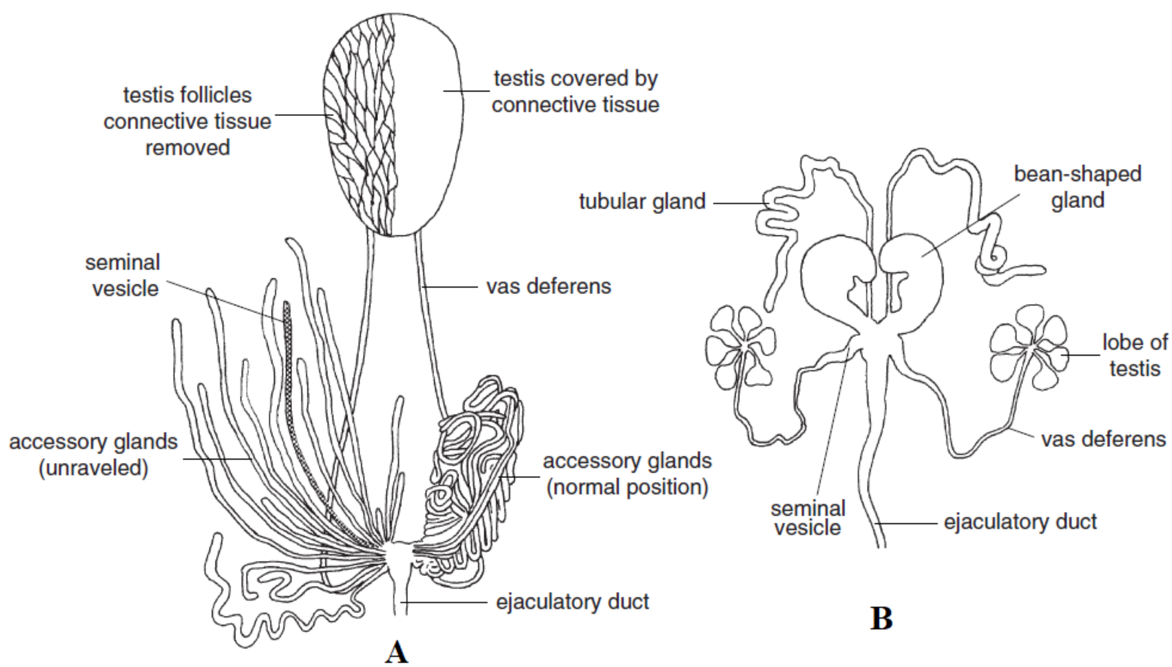

Fig. 10.1: Diagrammatic representation of male reproductive organs of (A) Locusta, and (B) Tenebrio showing various structures (Adapted from Chapman 2014).

(iv) Accessory glands. The accessory glands of male insects can be either ectodermal or mesodermal in origin and are hence referred to as *ectadenia* or *mesadenia*, respectively. The ectadenia open into the ejaculatory duct and are found in many Coleoptera and a few Diptera and Homoptera. The mesadenia open into the vasa deferentia or even in the distal end of ejaculatory duct, and occur in Orthoptera. However, both ectadenia and mesadenia are found in a few species of Coleoptera and Heteroptera.

10.3.2. FEMALE REPRODUCTIVE SYSTEM: The functions of the female reproductive system in insects is the egg production along with storing male's sperm until the eggs are ready for fertilization. The ovary is the major female reproductive organ, which is comprised of a cluster of eggs in the ovarioles, which consist of terminal filament, germarium, vitellarium, and a pedicel. The details of the components of female reproductive system are mentioned below:

(i) Ovaries: The female reproductive system is comprised of paired ovaries. The ovaries are usually somewhat compact bodies found on either side of alimentary canal in the body-cavity of abdomen (Fig. 10.2). Each ovary consists of separate egg-tubes or ovarioles of different numbers opening into the oviduct. The number of ovarioles in an ovary is uncertain and varies in different orders of insects. For example, the ovariole number does not exceed eight in cockroaches (*Periplaneta*). This number ranges between 5 to 7 in some species of orders, Thysanura (*Lepisma*) and Diplura. In a few anomalous instances ovarioles are wanting and the ovaries are more or less sac-like without any serial arrangement of the developing eggs. Such ovaries are well exhibited among Collembola. In some Braconidae (*Aphidius*) although there is an evident differentiation into follicles, ovarioles are wanting. This is a secondary and highly modified condition. Generally, the larger insect species within the group have a greater number of ovarioles than the smaller ones. Viviparous insect species show a smaller number of ovarioles in their ovaries. For example, the viviparous order Diptera, and a few insect species like *Hippobosca*, *Melophagus*, and *Glossina* contain only a couple of ovarioles in each ovary, while some aphids possess only one ovary with only one ovariole.

(ii) The Ovarioles: An ovariole is usually like an elongated tube consisting of the developing eggs in the form of a single chain, where one egg is behind the other. The oldest oocytes are found nearest to the oviduct. The wall of the ovarioles is in the form of a delicate transparent membrane, which is lined by the epithelial cells resting on the basement membrane, also known as **tunica propria**.

There are three zones or regions in an ovariole. The first region is ***the terminal filament***, which is a slender apical prolongation of the peritoneal layer. These filaments of the ovarioles of a single ovary get combined into a common thread that unites with that arising from the other ovary forming a median ligament. This median ligament maintains the ovaries in their position. However, in some insects, the median ligament is not present and the terminal filaments end in the body cavity. The second region of the ovariole is the ***germarium***, which forms the apex of the ovariole. It is found below the terminal filament, and is comprised of a mass of cells that later differentiate the primordial germ cells. The third region of the ovariole is the ***vitellarium***, which is the main part of an ovariole and it is comprised of the developing eggs along with nutritive cells (also known as nurse cells or trophocytes). The epithelial layer found on its wall grows inside to enclose each oocyte in the egg chamber or follicle. The cells of the follicle secrete the egg's chorion and may also nourish the oocytes.

There are three types of ovarioles depending on the presence or absence of nutritive cells along with their location.

(i) ***The paniostic type*****:** This type of ovariole doesn't have the specialized nutritive cells and only a string of follicles is present with oocytes getting nutrients from haemolymph *via* follicular epithelium *e.g.Periplaneta*. It is primitive and is largely found in the orders, Thysanura, Orthoptera, Odonata, Ephemeroptera, and Siphonaptera.

(ii) ***The polytrophic type***. In this type of ovariole, the nurse-cells are found, which alternate with the oocytes. In many insect orders, like Neuroptera, Hymenoptera and Coleoptera (Adephaga, the nurse cells are congregated in a bid to lie in chambers and each chamber is separated from the one containing an oocyte by a constriction. However, these constrictions are not found in some insect orders, like Lepidoptera and Diptera.

(iii) ***The acrotrophic type***. In this type of ovariole, the nurse cells are found and are located at the apices of ovarioles, e.g. in Polyphaga (Coleoptera) and Hemiptera. In some heteropterans, the nurse cells are linked with the oocytes with the help of cytoplasmic strands, also known as the trophic cords. Thus, types (ii) and (iii) are often clubbed as meroistic type of ovariole that is distinguished by the presence of nurse cells.

(iii) The Female Genital Ducts: The ovaries give rise to paired canals known as lateral oviducts that are generally formed from mesoderm. The two lateral oviducts connect with a common oviduct, which is primarily formed from the invagination of the body-wall behind the seventh abdominal segment, which however usually gets extended through the eighth abdominal segment to join the vagina. In many insects, no clear distinction occurs between these reproductive parts. In a few viviparous insects, e.g. *Glossina* and *Melophagus*, the vagina is enlarged forming a chamber or uterus for the reception of the immature stages. However, in most insects, it forms a genital chamber where the common oviduct opens. The bursa copulatrix, if present in some insects, is a pouch-like development of the vaginal region. It acts as a chamber that serves as a copulatory pouch during copulation or mating. The external opening of this chamber is known as the *vulva*. The vulva is narrow in numerous insects and the genital chamber turns into an enclosed pouch or tube, which is referred to as vagina. The vagina and oviducts are made of an epithelial layer, which rests upon a basement membrane and is coated outside with circular muscle fibres. In an immature insect, an epithelial plug cuts the ovariole's lumen from the oviduct but this plug is destroyed during first ovulation and consequently is replaced by follicular tissue's plug. In some orders, like Lepidoptera and Diptera, the ovarioles are opened together into an extension of the oviduct referred to as the calyx.

(iv) The Spermatheca (*receptaculumseminis*): The spermatheca is a single and sac-like organ or pouch with a slender duct, and usually has a diverticulum forming a tubular spermathecal gland. The spermatheca occurs in various forms and usually opens into the dorsal wall of the vagina by a duct. In numerous insects, where mating occurs only once and eggs get matured over a while then the spermathecae store the sperms and allow fertilization when eggs are matured with time to sustain fertile fecundity. The spermathecae are usually spherical or ovoid, or even tubular in some coleopterans, while branched in *Paederus*. It may occur as a single organ (as in *Blaps*, *Dacus* and *Phlebotomus*), two in *Culex*, and three in Calyptratae. It is derived from ectoderm, and hence is lined with dark or brightly coloured cuticle. In some insects, e.g. *Periplaneta*, the glandular cells are found on the wall of spermatheca, while a special spermathecal gland is found in other insects, which opens directly into the duct of spermatheca, or near its junction with the vagina. The gland or glandular cells may provide nourishment to the spermatozoa.

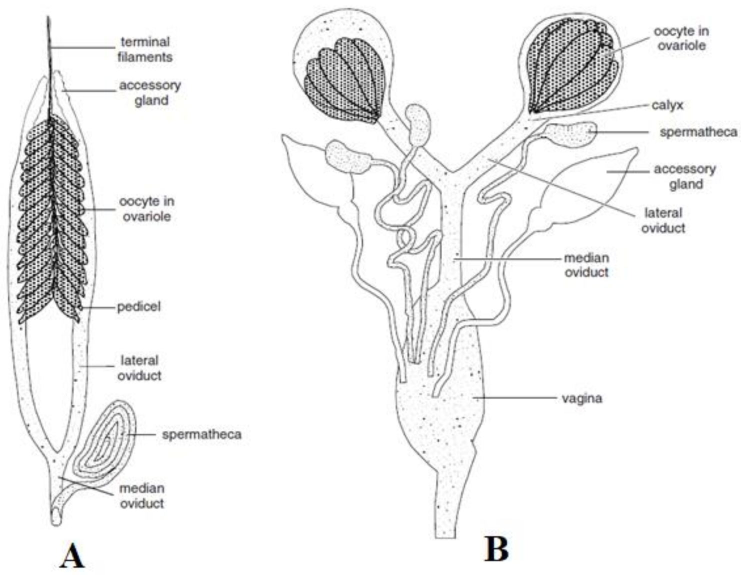

Fig. 10.2: Diagrammatic representation of female reproductive organs of (A) Schistocerca, and (B) Rhagoletis showing various structures (Adapted from Chapman 2014).

(v) The Female Accessory Glands: The accessory glands are also known as colleterial or cement glands due to their secretions that protect or cement the eggs to the substrate. For example, ootheca formation in *Periplaneta* and venom production in *Apis indica*. One or two pairs of accessory glands are found in most insect species, which generally open into the distal part of the vagina. These accessory glands are important organs in numerous Dictyoptera and Orthoptera, where they provide the material required for the formation of egg-pod or ootheca. In *Chironomus*, these glands secrete a mucus-like substance that forms a gelatinous investment of the eggs, while in Hyalophora they give a cement-like secretion that helps the eggs to stick to the substratum after being laid. The poison glands of hymenopterans, such as bees and wasps, are modified accessory glands.

10.4 SPERMATOGENESIS AND OOGENESIS

10.4.1. SPERMATOGENESIS

10.4.1.1. Structure of mature sperm

The sperm is usually flagellate in most insects and is about 300 µm in length and less than 1.0 µm in diameter (Fig. 10.3). It has a cell membrane, which is about 10 nm thick, coated by a layer of a glycoprotein called the glycocalyx. The sperm has a head region, whose greater part is occupied by a nucleus, which is homogeneous in appearance. The acrosome is present in front of the nucleus, which is a membrane-bound structure of glycoprotein. The acrosome is lacking in some insects, *viz*. Neuroptera. The acrosome is connected with the sperm attachment to the egg and its possible role in the lysis of the egg membrane, thereby permitting the successful entry of sperm. Each sperm has about 45–50 microtubules present in the form of a spiral encircling the central mass of chromatin. These microtubules run throughout the length of sperm and are concerned with sperm motility.

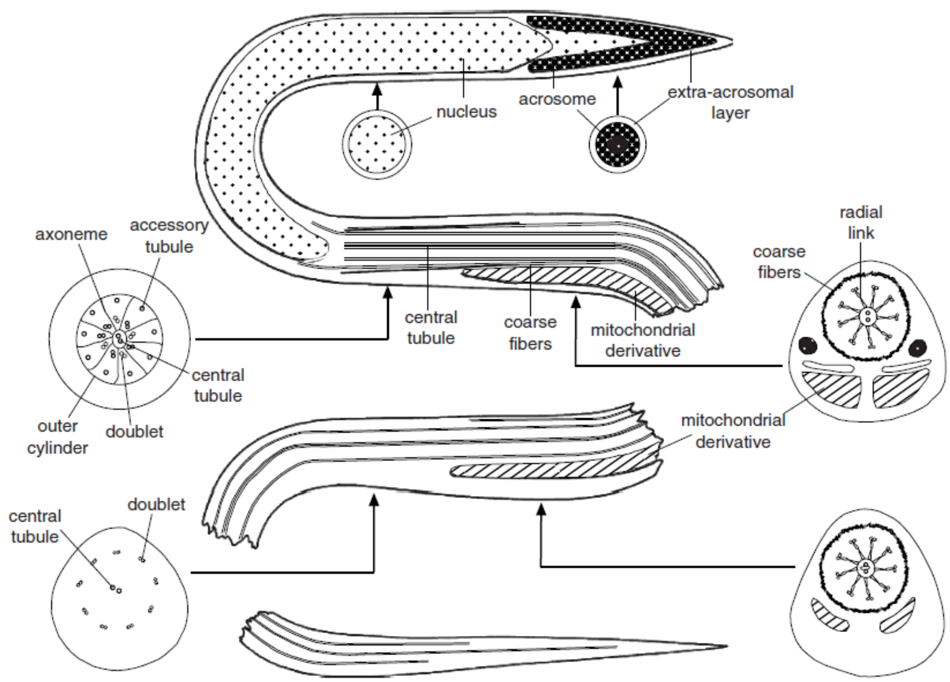

Fig. 10.3. Spermatozoa of an insect (Adapted from Chapman 2014).

10.4.1.2. Phenomenon of Spermatogenesis

The distal end of the testis follicle contains germarium, in which germ cells undergo division to produce spermatogonia. The spermatogonia are the cells that further undergo mitotic division to produce spermatocytes (Fig. 10.4). The spermatocytes then divide meiotically to produce spermatids. The spermatogonia in numerous insects, like those of orders, Homoptera, Orthoptera, Blattodea, and Lepidoptera obtain nourishment from an apical cell, while in some insects of orders, Diptera and Heteroptera, nourishment is provided by apical syncytium. Sooner, the apical connections are lost and spermatogonia get associated with other cells forming a cyst around them. Usually, one or even more spermatogonia get enclosed in a cyst. In some insects, two cyst cells are found around each spermatogonium, which probably provide nutrients to the developing sperm. There are three zones of development below the germarium, *viz*. (i) zone of growth, where primary spermatogonia within the cysts divide and grow in size to form spermatocytes, (ii) zone of maturation and reduction, where each spermatocyte undergoes two meiotic divisions to produce spermatids, and (iii) zone of transformation, where the spermatids develop into spermatozoa, which is also known as spermiogenesis. Usually, four spermatozoa are produced from one spermatocyte. However, in many insects, such as coccids the spermatids possessing heterochromatic chromosomes get degenerate and only two sperm are formed from each spermatocyte.

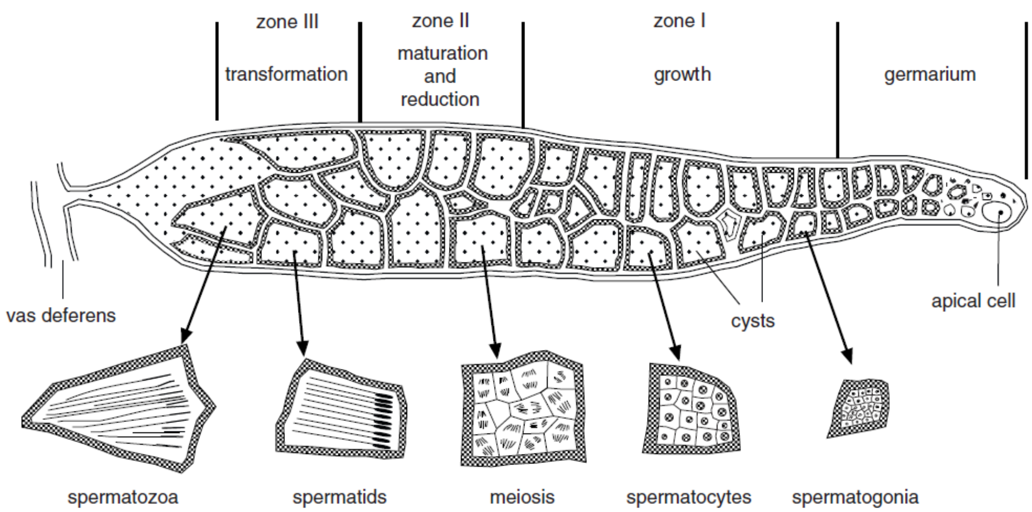

Fig. 10.4. The diagrammatic representation of the testis follicle showing the stages of development of the sperm (Adapted from Wigglesworth, 1965).

10.4.1.3. Spermiogenesis: The spermatid produced after meiosis is generally a rounded cell with normal cell organelles. It undergoes several changes and gets modified into a motile sperm, which is known as spermiogenesis. This process can be better understood by studying the organizational changes in each cell organelle of mature sperm.

(i) Acrosome. The acrosome is largely formed from Golgi bodies, which are scattered throughout the cytoplasm of spermatocytes in the form of 30–40 dictyosomes. After the second meiotic division, the fusion of all dictyosomes into a single body occurs (as in *Acheta*), which is known as **acroblast**. In later spermatid, a pro-acrosomal granule appears in cup of acroblast and grows in size. The acroblast migrates with its open side toward the nucleus, and then the granule moves toward the nucleus and gets attached to it. With the elongation of cell, the acroblast membranes move towards posterior side of the spermatid and the membranes are sloughed off along with much of the cytoplasm and other cell inclusions. Thereafter, the pro-acrosomal granule becomes cone-shaped and transforms into an acrosome.

(ii) Nucleus. In early spermatid, the nucleus seemingly has a typical interphase unoriented structure. With the development of the sperm, the nucleus gets elongated and the chromosomes get aligned almost parallel to the axis. The nucleoplasm gets highly reduced until the entire nucleus appears to comprise a homogeneously dense material.

(iii) Mitochondria. The mitochondria fuse into a single large body known as the **nebenkern**, which consists of an outer membrane and a central pool of mitochondrial components. The nebenkern gets detached into two mitochondrial derivatives connected with a developing axial filament just behind the nucleus. They become elongated forming a pair of ribbon-like structures. Simultaneously, their internal structure gets reorganized, and the cristae form a series of parallel lamellae at one side and paracrystalline material replaced the matrix.

(iv) Centriole and axial filament. Two centrioles are present in young chromatid, which are oriented at right angles and are composed of nine triplets of tubules. One centriole gives rise to axial filament and finally both centrioles disappear. The tubules of axial filament come out from the centriole and extend to the length of sperm’s tail. The accessory tubules grow from tubule doublets, which appear first as side arms. These become C-shaped and get detached and close up to form cylinders.

Biochemical changes: Large quantities of DNA and RNA are synthesized due to repeated cell divisions during spermatogenesis. However, DNA synthesis stops in the early spermatid just before meiosis, while RNA synthesis continues. Later on, both the syntheses stop and RNA is eliminated from the nucleus and the cell as the nucleus elongates. This is associated with the growth in arginine-rich histone production forming a complex with DNA, which refrains DNA from acting as a primer during RNA synthesis, and insulates the genetic material from enzymatic attack during transit to the egg.

10.4.2 Oogenesis

Each ovariole is comprised of a distal germarium, where oocytes are produced from oogonia, and vitellarium in which yolk is deposited. These two components reflect two phases of oocyte growth. The vitellarium forms the greater part of the ovariole, while the germarium is composed of prefollicular tissue, stem line oogonia and their derivatives. The stem line oogonia are formed directly from the germ cells and during division one daughter cell becomes a functional stem line cell, while the other becomes an oogonium, which thereafter develops into an oocyte. The oocytes then get enlarged and passed down the ovariole and are covered by prefollicular tissue that forms the follicular epithelium as the oocyte leaves the germarium. At first, this could be 2- or 3-layered, but finally develops into a single layer of cells. The growth of the oocyte continues and the cells of follicular epithelium become cuboid or columnar. The oocyte’s growth is very fast during yolk accumulation but no further division occurs in the follicle cells and they form flattened squamous epithelium stretched over the oocyte. However, nuclear division perhaps continues in the follicle cells making them binucleate or endopolyploid, thereby allowing high levels of synthetic activity in them. The follicle cells then start producing some minor yolk proteins along with some enzymes involved in yolk processing. These cells also produce ecdysone or its precursor, which gets accumulated in the oocytes of some insects. They also produce vitelline envelope and ligands required to determine the terminals of the embryo along with its dorsal–ventral axis. Finally, these cells also produce egg shell or chorion.

DifferentmRNAs, ribonucleoproteins, ribosomes and other major constituents are transported to the oocyte during the early stages of its growth. In polytrophic ovarioles, all the contents of cytoplasm are transported to the oocyte when the trophocytes collapse. This movement of material from trophocytes into the oocyte is along an electrical potential gradient. The difference in the electric charge between the oocyte and trophocytes modulates the movement of charged molecules electrophoretically and thus contributes to this movement of various materials into the oocyte. The final collapse of trophocytes is seemingly mediated by contractile units inside the cells, which probably force them into the oocyte.

Meiosis: Meiosis starts very early in the development of oocytes in a majority of insects, but reduction divisions are not completed inside the ovary, as oocytes generally leave ovarioles in the metaphase stage. Meiosis did not proceed beyond the first prophase until ovulation in *Locusta,* and it resumes during insemination. In *Locusta*, the ecdysone from the follicle cells stimulates the further continuation of meiosis to which the oocyte is very sensitive just prior to the formation of chorion or chorionogenesis. The resumption of meiosis, in *Drosophila*, is triggered by ovulation through some hydration effect.

10.5 MATING

Mating in insects is characterized by a series of events, which involves mate-recognition, courtship and mating (copulation). The recognition of a mate is directed primarily by olfactory cues in the form of odours, such as pheromones (or sex-pheromones), which usually are secreted by the adult females and are perceived by the males with the help of sensillae present on the antennae (primarily) and mouth parts (secondarily). This is followed by courtship where males used to court the females by performing various displays. However, this courtship is dependent on many factors, like age and sexual status, and is lacking in many insect groups.

Mating is characterized by copulation, *i.e.* insertion of male genitalia into that of the female. When the two sexes meet, the male may either directly go for copulation with the female or may exhibit courtship behavior, as reported in some species, during courtship, the male will stimulate the female through olfactory, acoustic, visual, and/or tactile means, in a bid to appease the female for copulation. Thereafter, the male usually mounts onto the female's back. However, the reverse is also reported, where the female mounts on the back of the male, as in the case of some cockroaches, gryllids and tettigoniids. During pairing, the male insect often grasps the female insect with his feet. Some male insects, such as *Ammophila*, hold the females with their mouthparts, like mandibles. The legs of males are modified to grasp the females in some insects. For instance, forelegs of *Dytiscus* bear suckers, middle femora of *Hoplomerus* (Hymenoptera) bear spines, and hind femora of male *Osphya* (Coleoptera) are so modified to grip the female's elytra and abdomen. Male fleas, collembolas and biting lice hold their females using their modified antennae. Copulation can occur immediately after the genital contact of insects or there may be a considerable interval before they copulate, also known as latent period. The vigorous shaking of genitalia is also observed in many insects, like in the seven-spotted ladybird, *Coccinella septempunctata*, which are known as bouts, however, these bouts are lacking in many insect species within the same family. The details of copulation differ from group to group in many insects and are dependent on the structure of genitalia.

Some insects, like *Crocothemis*, copulate and transfer sperm in the flight and their copulation is very brief, which may last for even less than 20 seconds. However, many other insect species used to settle before going for copulation, and their mating duration could be from a few minutes to many hours, as in the case of ladybird beetles. In mosquitoes, the mating is complete within a few seconds, while it may last for a few hours in *Oncopeltus* and *Propylea dissecta*. In *Nezara*, the mating may even last for 1–2 days, when there is a female population dominating the male ones, and this duration could be extended to seven days if the males are in the majority. Extended copulations may also serve the purpose of mate-guarding, as reported in a ladybird beetle, *Menochilus sexmaculatus*, where adult male just mount on the back of female to guard her and protect her from other males.

10.6 INSEMINATIONS

In insects, sperm transfer (insemination) is a separate process from the fertilization of eggs, which in some cases takes many months to years. During this period, the female's spermatheca stores the sperm. Sperm can also be transferred in a spermatophore or may pass directly into the spermatheca without using a spermatophore. They may even pass into the female's bursa copulatrix from which they move inside the spermatheca.

Spermatophores: It is a primitive method of insemination that involves the production of a spermatophore by the male insects (Fig. 10.5). It is a capsule in which the sperm are transferred to the female. These spermatophores are reported in some insect orders, *viz*. Orthoptera, Blattodea, Neuroptera along with some Coleoptera, Heteroptera, Hymenoptera Trichoptera, Diptera and Lepidoptera.

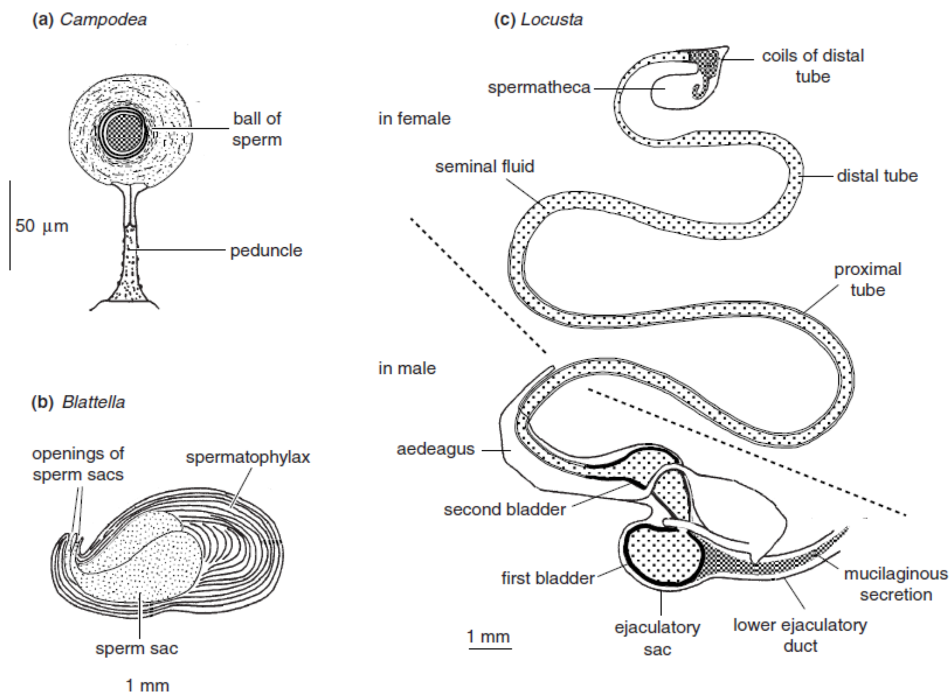

Fig. 10.5.: Diagrammatic representation of various spermatophores.

The spermatophore contains some drops of sperm-containing fluid. The spermatophores of Diplura are produced in absence of the female. The sperm can live in a spermatophore for about two days. A male can produce 200 spermatophores in a week. In Pterygota, spermatophores are transferred directly from male to female. Spermatophore is produced from secretions coming from glands of male’s reproductive system. It is usually produced the accessory glands, but in the absence of these glands, it is produced by the gland in the ejaculatory duct.

Sperm transfer to spermatheca. The sperm are transferred to the spermatheca and are stored just after the transfer of the spermatophore. The sperm can escape from the sperm sac through a pore, but when the sperm sac is fully enclosed within the spermatophore, they can escape only after the rupturing of the spermatophore. This movement of sperm to spermatheca can be either active or passive. In numerous insects, the spermatophore is placed in bursa copulatrix of female and the sperm transfer to spermatheca is seemingly occurred due to the contractions of female ducts. Females of some insect species used to eject the spermatophore after insemination, for example, *Blattella* and *Rhodnius*, which drop the spermatophores after 12 and 18 hours of copulation, respectively. Some female insects used to eat these spermatophores, e.g. *Sialis* and some ladybirds.

Direct insemination: There are many insect groups of insects where sperm is transferred directly without any spermatophore or sperm packet. Here, the sperm are directly transferred to bursa copulatrix of the female and also into the spermatheca. This direct insemination process occurs in some species of orders, Mecoptera, Trichoptera, Heteroptera, Hymenoptera, Diptera and Coleoptera.

10.7 OVIPOSITION

The process of laying eggs is known as oviposition. Insects lay eggs using a slender structure found at the terminal end of the abdomen known as the ovipositor. However, in many insects, this structure is lacking. In a few insect groups, the terminal abdominal segments are long and telescopic and are shaped into an ovipositor which is meat to lay eggs or oviposition, e.g. Hymenoptera and Diptera. In *Musca*, the telescopic structure is formed from segments 6–9, where sclerites of ovipositor are highly reduced to rods. Ovipositors in some insect orders, like Thysanura, Heteroptera, Thysanoptera, Odonata, Homoptera, Orthoptera, and Hymenoptera are derived from the appendages found in abdominal segments 8 and 9. The terminal abdominal segments and ovipositor have mechanoreceptors and a small number of chemoreceptors.

10.7.1. Mechanisms of oviposition: The eggs are simply laid on the surface in the species lacking an ovipositor, while those species lay eggs in the host or crevices, where the terminal segments of the abdomen are telescopic. Numerous species with an ovipositor made from the appendages of segments eight and nine penetrate tissues, akin to that of the sting mechanism of *Apis*. In an ichneumon parasitoid, the abdominal tip is turned down during the start of oviposition. The intersegmental muscles are also involved during oviposition and are stretched. For example, the abdomen of *Anacridium* stretches from 3–5 cm to almost 10 cm and *Schistocerca* can dig deep inside about 14 cm. The ventral valves of the ovipositor during digging, lever the abdomen downwards and the upper valves push the soil away. The pull generated by ventral valves is transmitted to abdomen resulting in extension of intersegmental membranes between abdominal segments four and seven. The female partially withdraws her abdomen at intervals during digging. The eggs are firstly passed out micropylar-end and thereafter the abdomen is gradually withdrawn as more eggs are oviposited. After entire oviposition, the female covers the upper part of hole with a frothy plug and scrapes the soil over the top with her hind tibiae after withdrawing her abdomen. This entire process takes about two hours, of which, oviposition process takes about 20 minutes.

10.7.2. Control of oviposition: The readiness to oviposit is affected by copulation. For example, a female *Bombyx* lays all her eggs within a day after mating, while a virgin retains most of her eggs for a few days. Under normal conditions, primarily peptides transferred to female during sperm transfer induce the female to search for an oviposition site and to begin ovipositing. In grasshoppers, muscles activity regulates of movement the ovipositor valves by the central pattern generator found in terminal abdominal ganglion. In non-ovipositing insects, the pattern generator activity is inhibited by neural activity from the head ganglia and metathoracic ganglion. The octopamine is also needed for normal functioning of muscles and to maintain the activity of central pattern generator.

10.7.3. Role of accessory glands: The role of female accessory glands is usually to fix eggs in position or save them from predators and desiccation. Some insects attach their eggs close to the food source. Some insects, *e.g.* lepidopterans, lack accessory glands and drop their eggs from the air. However, well-developed glands are found in species that cover their eggs with secretion. The secretions from accessory glands of numerous aquatic insects form a gelatinous mass covering the eggs.

10.7.3.1. Oothecae. Numerous species of insect groups, viz. Mantodea, Blattodea, and Acridoidea, oviposit in oothecae formed by secretions of female accessory glands. These have precise and characteristic forms which allow respiration by eggs and the escape of newly hatched larvae and simultaneously protect them from desiccation and predators.

10.7.3.2. Interactions with male-derived proteins. The accessory gland products can interact with proteins formed from male accessory glands and sperm. The accessory gland secretion of female muscid flies contains proteolytic enzymes and an esterase which play important roles in egg-fertilization, as they break the acrosomal membrane of sperm, and facilitate the digestion of a cap over micropyle. The accessory gland products of female Scatophaga are secreted during copulation, which is required in greater quantities to process larger quantities of sperm and seminal fluid.

10.8 SPECIAL MODES OF REPRODUCTION

Reproduction in insects generally involves the meeting of the two sexes leading to fertilization, as also occurs in other animals. However, there are numerous exceptions to this, as there are a few special modes of reproduction in insects, which are mentioned below:

10.8.1. Viviparity – Insect species in which the entire embryonic development is completed in the mother's body and thereby producing larvae or nymphs rather than laying eggs are known as viviparous. Viviparity is largely reported in Aphidoidea, Strepsiptera and 'Pupiparan' Diptera. It is somehow more than the retention of eggs in the female reproductive tract and the expulsion of young ones rupturing the chorion. There are four main types of viviparity:

10.8.1.1. *Ovoviviparity.* In this type of viviparity, there is enough yolk in the eggs to provide nourishment to the developing embryos, which the mother has deposited soon after hatching. Special nutritive structures are lacking in this case though the chorion is thin and the female might have a lesser number of ovarioles. Ovoviviparity usually occurs in some insects of Blattidae, Muscidae, Tachinidae,Thysanoptera, and Coleoptera.

10.8.1.2. *Adenotrophic viviparity.* In this case, the thin chorionated eggs are singly ovulated and the embryos are developed at the cost of yolk. Larva when hatched degenerate with their guts closed posteriorly, which is retained in the muscular vagina of the mother. There the larva feeds on the secretion of the mother's uterine glands and undergoes two moulting and is deposited as a fully mature larva that very soon pupates. This type of viviparity is found in *Glossina* and 'Pupiparan'.

3. Haemocoelous viviparity. It is a more specialized type of viviparity that is found in paedogenetic larvae of Cecidomyiids *Mycophila, Miastor,* and *Heteropeza*, and in Strepsiptera. In this case, oviducts and ovaries don't lie free among the fat body, which breaks up when mature and the eggs are dispersed in haemocoel. These eggs lack chorion and are surrounded by a trophic membrane through which nutrients from the maternal tissues are supplied. The young larvae after completing development escape through the brood canal of the mother, in the case of Strepsiptera, but the larvae of cecidomyiids first feed on maternal tissues before leaving through its integument.

4. Pseudoplacental viviparity. In this type of viviparity the embryo develops in the enlarged vagina of the mother from a yolkless egg that is almost lacking chorion. Here, placenta-like structures formed from maternal or embryonic tissues nourish the embryo, while oral feeding is lacking. It occurs in Polyctenidae, Aphidoidea, Blattidae, Psocoptera and in a few Heteroptera.

10.8.2. Parthenogenesis: In parthenogenesis, the unfertilized eggs undergo full development, and is well exhibited in many insects, *e.g.* drones in honey bees and some lepidopterans. This phenomenon could be facultative, when it occurs with bisexual reproduction, or even obligatory when males are functionless, absent or extremely rare. The parthenogenetically developing eggs can either have haploid or diploid set of chromosomes giving rise to either both sexes (*amphitoky*), or only males (*arrhenotoky*) or females (*thelytoky*). Parthenogenesis can even co-occur in the life-cycle with viviparity and paedogenesis. Some examples of parthenogenesis are mentioned below.

1. *Haploid facultative arrhenotoky.* In this type of parthenogenesis, a sex-determining mechanism can be more flexible than the usual chromosomal type. The females lay fertilized eggs (diploid) giving rise to females and unfertilized eggs (haploid) develop into males. It occurs in Hymenoptera along with some species of aleyrodids, Coccoidea, and Thysanoptera.

2. Facultative thelytoky. This type of parthenogenesis oogenesis is followed by meiosis and after fertilization, both males and females are produced. However, the eggs which are left unfertilized can attain diploidy by fusing with a polar body and thereby develop only into females. This phenomenon is well observed in some types of *Coccus hesperidum,* Tetrigidae and Symphytan Hymenoptera.

3. Obligate thelytoky. This is a common type of parthenogenesis, where males are extremely rare, non-functional, or absent. Here, the eggs are usually formed without meiosis, also known as apomictic parthenogenesis, and doubling of the chromosome number occurs due to fusion of cleavage nuclei and a polar body. Obligate thelytoky allows fast reproduction by focusing all the female’s activity on feeding and reproduction of young ones thereby eliminating male interferences. It is prevalent in some Curculionidae and psychids.

4. Cyclical parthenogenesis. Striking examples of obligate thelytoky are evident in most of the aphids and cynipids, which are exclusively parthenogenetic. However, a bisexual generation is interposed on the remaining ones occurring in the cold season. In Aphidoidea, usually many parthenogenetic generations occur with obligate thelytoky, which is followed by a sexupara generation, which later gives rise to bisexual generation giving rise to both males and females. This is known as Cyclical parthenogenesis. In *Phylloxera,* two kinds of females occur which parthenogenetically produce males and females. In Cynipid, one parthenogenetic generation alters with one sexual generation, where the former generation consists of two kinds of females, which produce respective males and females. Cyclical parthenogenesis thus has a synergistic effect on the propagation of species by possessing genetic advantages of bisexual reproduction with a greater reproductive rate due to thelytoky.

A rare phenomenon of gynogenesis or pseudogamy also occurs, which is very similar to parthenogenesis. Here, the sperm only activates the egg without the fusion of nuclei and thereby no genetic material is contributed to the progeny, e.g. a moth, *Lujjialapidella*. Similarly, a bisexual beetle, *Ptinusclavipes*has a triploid gynogenetic form female known as *mobilis,* which lays fertile eggs after copulating with a *clavipes*male.

10.8.3. Paedogenesis – Paedogenesis occurs when the immature stages of insects have functional ovaries and their eggs may develop parthenogenetically. It occurs in some cecidomyiids, *viz*. *Heteropeza*, *Miastor*, *Mycophila*and a coleopteran, *Micromalthus debilis.* Two kinds of paedogenetic larvaeare reported in a North American species of *Micromalthus*.One of them is the reproductive form, which produces viviparously 4-20 larvae, who later on consume their parent and escape to lead a phytophagous life. These larvae then develop either into adult females or paedogenetic larvae similar to their parents or the second form of paedogenetic larva, which can lay a single egg that’s developed into a male, who during its larval form also consumes its parent. However, both males and male-producing larvae are not found in the South African type of this species. In *Heteropezapygmaea,* apart frommales and females (which can lay both fertilized and parthenogenetic eggs), there exists three kinds of viviparous paedogenetic larvae. The first kind of larva can produce daughter-larvae which may develop into (a)adult females, (b)paedogenetic larvae, (c)purely male-producing paedogenetic larvae and (d)the third kind of paedogenetic larvae which can give rise to adult males or the paedogenetic larvae of the first kind.

Most aphids are also considered paedogenetic, as their earliest offspring begins during embryonic development, which is long before the mother is mature. Some of the mothers are even born pregnant. Similarly, fertilization and early embryonic development in the mother before her final moulting occurred is also reported in *Hesperoctenes*(Polyctenidae). Occurrence of oviparous pupal paedogenesis in chironomids is also reported, where parthenogenetic eggs are laid by a fully-formed adult that is still enclosed in the pupal integument.

10.8.4. Polyembryony: Polyembryony occurs when two or more embryos are produced from a single egg by subdivision, which is mostly found in parasitic insects (*e.g.Platygaster*). It is often considered an abnormality and is reported in several many insects, *viz*. *Ageniaspis, Copidosoma*, and *Litomastix* of family Encyrtida, in *Platygaster*of family Platygasteridae, in *Amicroplus*and *Macrocentrus* of familyBraconidae. In this case, the nutrition for numerous developing embryos is provided by the host's haemolymph *via* a specialized enveloping membrane known as *trophamnion* and is not solely dependent on the original egg. When the embryos are numerous, they are surrounded by trophamnion, which is in the form of an elongated, irregularly shaped mass called an embryo chain. This embryo chain gets broken up and liberates the embryos giving rise to first-stage larvae. The abortive embryos along with degenerate larvae and trophamniotic fragments are later on eaten by the surviving larvae, which may otherwise consume the host tissues to attain maturity in their late larval, pupal or adult stage. Thus, a single host is capable of producing a brood of two to 3000 parasites. This brood, as a result of superparasitism, is composed of either one or both sexes. Polyembryony can supposedly achieve an enormous reproductive potential but it loses its effects as the females of polyembryonic species produce fewer eggs as compared to those females laying monoembryonic eggs.

10.9 SUMMARY

Insects have the high reproductive capacity and are the most successful group of living organisms on this planet. The male reproductive system is mainly associated with the production

and storage of sperm. The male reproductive system consists of paired testes, vasa deferentia, seminal vesicle, ejaculatory duct, male genitalia or aedeagus, and accessory glands. The female reproductive system in insects is related to egg production, storing the male's sperm and propagating the progeny. The female reproductive system includes the ovaries, ovarioles, female genital ducts, spermathecae, and accessory glands. The eggs and sperm are the products of spermatogenesis and oogenesis, respectively. Mating in insects is characterized by a series of events, which involves mate recognition, courtship, andcopulation. Insemination in insects has been mediated with the help of a spermatophore. However, direct sperm transfer without using a spermatophore is also a highlight of many insect orders. The process of laying eggs is also known as oviposition. Insects lay eggs using a slender structure found at the terminal end known as the ovipositor. However, in many insects, this structure is lacking. The oviposition in insects can be regulated by many factors. There are four special modes of reproduction in insects apart from sexual reproduction, viz. viviparity, parthenogenesis, paedogenesis, and polyembryony.

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10.11 TERMINAL QUESTIONS AND ANSWERS

Question No.1 Explain the structure and modification of male reproductive organs in insects.

Question No.2 Describe the structure and modification of female reproductive organs in insects.

Question No.3 Give a detailed account of mating behaviour in insects.

Question No.4 Explain in detail the phenomenon of spermatogenesis in insects

Question No.5 Discuss the phenomenon of oogenesis in insects.

Question No. 6 Explain oviposition in insects.

Question No. 7: Discuss various mechanisms of sperm transfer in insects.

Question No. 8: Describe various special modes of reproduction in insects.

UNIT 11: NEUROENDOCRINE SYSTEM

CONTENTS

11.1 Objectives

11.2 Introduction

11.3 Neuroendocrine System in Insects

11.4 Role of Neurosecretion in Various Metabolic Activities

11.5 Metamorphosis and Development of Insects

11.6 Summary

11.7 Terminal Questions and Answers

11.8 References

11.1 OBJECTIVES

After reading this unit, the student will be able to:

- Understand about the neuroendocrine system in insects.
- Learn different neurohormones in insects.
- Understand the role of neurosecretion in insect metamorphosis & development.
- Effect of neurosecretion in various metabolic activities of insects.

11.2 INTRODUCTION

In the previous unit, we discussed about the reproduction in insects, including the details of the male and female reproductive organs. Mating in insects involves series of events, like mate recognition, courtship, copulation, insemination, oviposition etc. There are four special modes of reproduction in insects apart from sexual reproduction, viz. viviparity, parthenogenesis, paedogenesis, and polyembryony. In this unit, we discuss neuroendocrine systems, which can be defined as the sets of neurons, glands, non-endocrine tissues, the neurochemicals, hormones, and humoral signals whichinsects produce and receive, that function in an integrated manner to collectively regulate a physiological or behavioural state. Nervous system regulates all physiological requirements of an insect including growth, reproduction, and protein formation through the endocrine system via hormones. Hormones complement the nervous system, which provides short term coordination, and the activities of both systems are closely linked.

Hormones: Chemical substances that are transported in the insect's body fluids (haemolymph) that carry messages away from their point of synthesis to sites that where physiological, behavioural and developmental processes are influenced.

In insects, neurosecretory cells are numerous and have important functions. Recent work has revealed that there are two types of neurosecretory cells: type A which stain with para-aldehyde fuchsin, and type B which do not. All cells possess electron dense granules. The neurosecretory cells can pro-duce blue colour from the reflected light due to the light scattering effect of colloidal-sized particles.

(a). Moulting hormones: are ecdysteroids (Fig. 11.1) which, in immature insects, are produced by the prothoracic glands. In most adult insects the prothoracic glands degenerate, but gonadal and other tissues may produce ecdysteroids. In most insects, as in *Drosophila melanogaster* (Diptera), the main ecdysteroid secreted is ecdysone. Ecdysteroids act on the epidermis to promote moulting. Ecdysone is generally considered to be a prohormone, being converted in the fat body or epidermis in most insects to the active hormone 20-hydroxyecdysone, by a cytochrome P450 enzyme CYP314A1, encoded by the gene shade. It remains possible, however, that ecdysone itself may have actions distinct from those of 20-hydroxyecdysone.

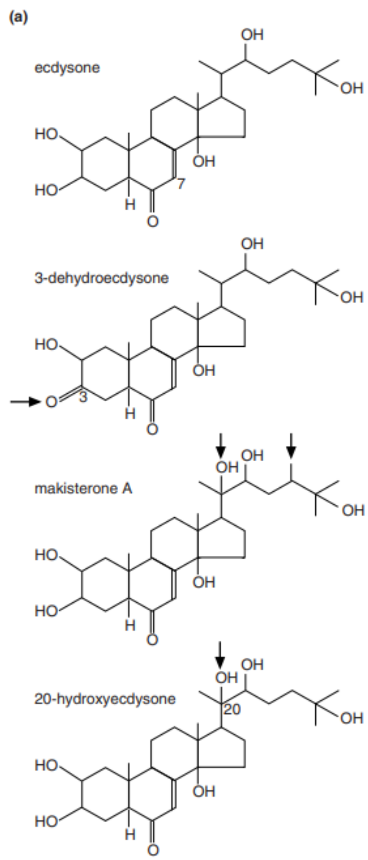

Fig.11.1: Ecdysteroids. Structures of ecdysone and related ecdysteroids produced by insects. Arrows indicate differences from ecdysone. Numbers relate to positions of carbon atoms.

(b). Juvenile hormone:

Juvenile hormone is produced by the corpora allata. Chemically, the hormone is methyl 10-epoxy-7-ethyl-3, ll-dimethyl-2, 6-tridecadienoate in moth *Hyalophora cecropia* (Fig. 11.2). It is likely that considerable species variability may be found in chemistry of this hormone since the corpora allata vary in functional importance.

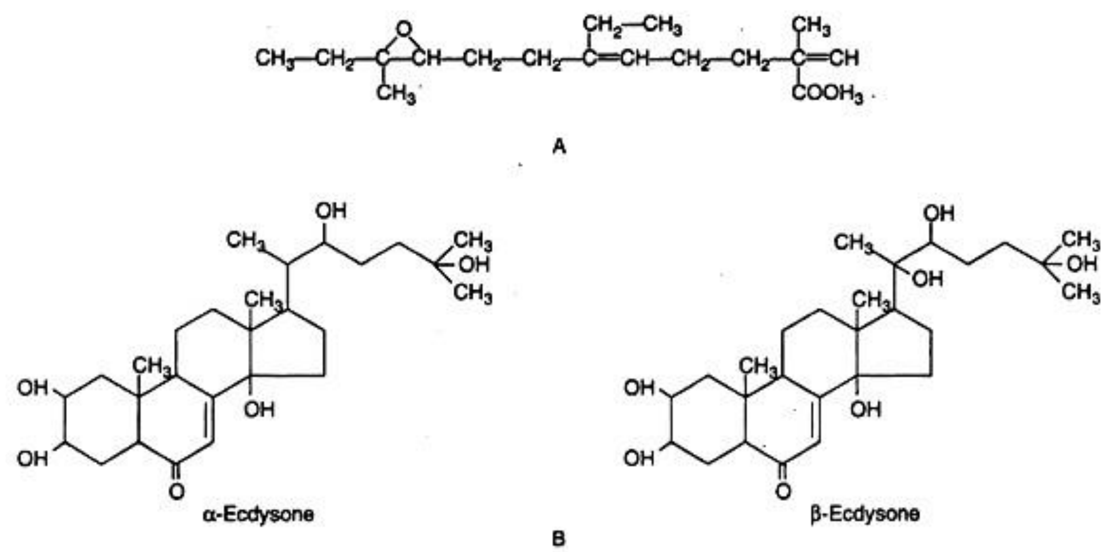

Fig.11. 2: A Structure of Juvenile hormone B. Structure of ecdysone.

11.3 NEUROENDOCRINE SYSTEM IN INSECTS

The endocrine organs of insects are of two types (most of which are within the central nervous system):

1) Neurosecretory cells within the central nervous system

2) Specialized endocrine glands such as the corpora cardiaca, corpora allata, and the prothoracic glands

1) Neurosecretory Cells: Neurosecretory cells normally occur in the ganglia of the CNS. They appear like typical nerve cells with axons, but they show cytological evidence of secretion. These secretions may act directly on effector organs or they may act on other endocrine glands, which in turn are stimulated to secrete their hormones. There may be neurosecretory cells in both the brain and in the other ganglia, located in the protocerebrum of the insect brain is a group of cells which produce "brain hormone." Brain hormone is also called neurosecretory substance.

This hormone, once synthesized in the brain, moves along nerve cells to an endocrine gland called the corpus cardiacum, where it is stored. The corpora cardiaca are paired endocrine glands which usually lie embedded in the wall of the aorta in the head region of the insect.

The most common hormones that are secreted by these cells are:

- **Ecdysiotropin** (Protocerebrum secretes ecdysiotropin or prothoracicotropic hormone (PTTH) or brain hormone (BH) that acts on ecdysial glands).
- **Bursicon** (Tanning hormone): triggers the tanning or darkening of adult cuticle.
- **Eclosion hormone:** It is stored in the corpora cardiaca and is released into the blood at the time of switchover from pupal to adult stage initiate the pre-eclosion behavior.

2) Specialized endocrine glands:

(a). Corpora Cardiaca: The corpora cardiaca are a pair of organs often closely associated with the aorta, and often forming part of its wall. In higher insect groups, they have become separated from the aorta. They are absent in Collembola. Each organ contains the endings of axons from cells in the brain and other axons passing through to the corpora allata. They also contain glial cells. They store and release hormones from the neurosecretory cells of the brain to which they are connected by 1 or 2 pairs of nerves. In addition, the intrinsic secretory cells produce hormones, which are concerned with the regulation of the heartbeat. At certain times in the insect's development, the brain hormone is released from the corpora cardiaca into the hemolymph. Once in the hemolymph, the brain hormone is carried to a special target organ, the prothoracic gland, so called because it normally is located in the prothoracic region of the insect.

(c). Prothoracic Glands: The prothoracic, or thoracic glands are a pair of diffuse glands at the back of the head or in the thorax, but in the Thysanura they are at the base of the labium. The prothoracic gland is stimulated by the brain hormone to produce another hormone called moulting hormone, also known as ecdysone. In most insects, these glands break down soon after the final moult to adult (exceptions: Thysanura which continue to molt after become adults, and some grasshoppers). Ecdysone is then transported by the hemolymph to specialized cells in the epidermis known as molting fluid cells. These cells are stimulated by ecdysone to produce the moulting fluid. Moulting fluid contains enzymes which digest away a portion of the old cuticle and aid the insect in the moulting process.

A new cuticle is then secreted by the epidermal cells. Prior to its completion, the insect will split the old exoskeleton at weak points called ecdysial sutures, which are located in the head and thoracic areas. The splitting of the exoskeleton may be accomplished by taking in air and then muscle contraction which produces pressure along the ecdysial sutures. The insect will then crawl out of the old exoskeleton, and, by taking in air, stretch the new exoskeleton to a larger size before hardening of the new cuticle takes place.

(d). Corpora Allata: (Fig.11.3) They allata are glandular bodies, usually one on either side of the oesophagus although they may be fused into a single median organ in some Diptera. In the Thysanura, they are at the bases of the maxillae. Each is connected to the corpus cardiacum on the same side, and also each is connected with the suboesophageal ganglion. The hormones secreted by the corpora allata are referred to as juvenile hormones or "JH." As the name implies, these hormones maintain juvenile and immature characters within the developing insect.

Through, the interaction and the levels of juvenile hormone and ecdysone, insect growth and metamorphosis are regulated. When these hormones are present in sufficient quantity in the body, growth and moulting occur, but juvenile hormone tends to keep the insect in immature stages by affecting genes which express the larval characters. In a later instar, juvenile hormone levels decrease and adult tissues differentiate under the influence of ecdysone, and their levels, insect growth and metamorphosis are accomplished.

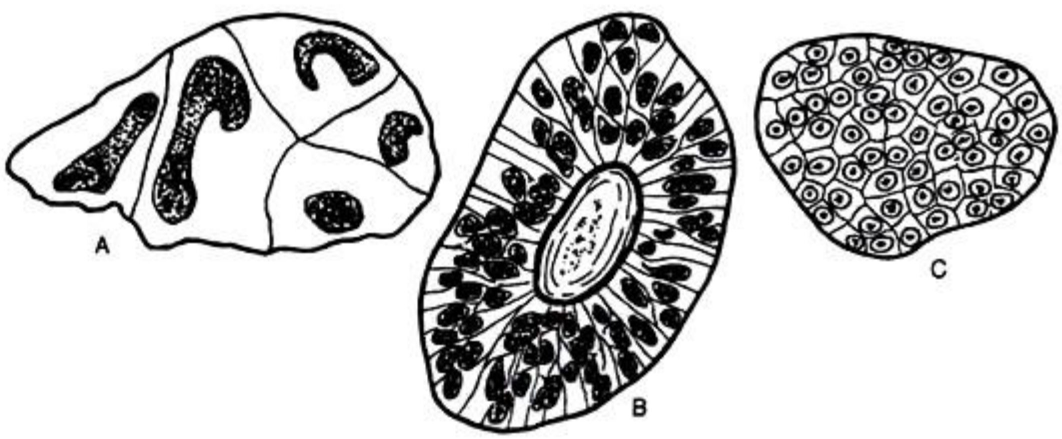

Fig. 11.3: Histological structure of corpora allata of different insects: A, Pieris brassicae, few large cells with polymorphic nuclei; B,Pentatomarufipes, an almost syncytial mass of small cells C, bacillus rossii, a nearly columnar epithelium surrounding the embryonic lumen.

11.4 ROLE OF NEUROSECTRETION IN VARIOUS METABOLIC ACTIVITIES

Insect hormones and neurohormones have been studied with respect to their involvement in a number of general physiological functions (Fig. 11.4). Specifically, hormones and neurohormones influence development, diapause, mating and oviposition, metabolism, development of nervous sys-tem, control of circadian rhythms, regulation of dormancy, pheromone production and regulation of migratory behaviour. Regulation of Moulting, Determination of form at Metamorphosis, Polymorphism, Regulation of Diapause, Involvement in Reproduction, Regulation of Metabolic Activities and general body functions, Regulation of Behaviour.

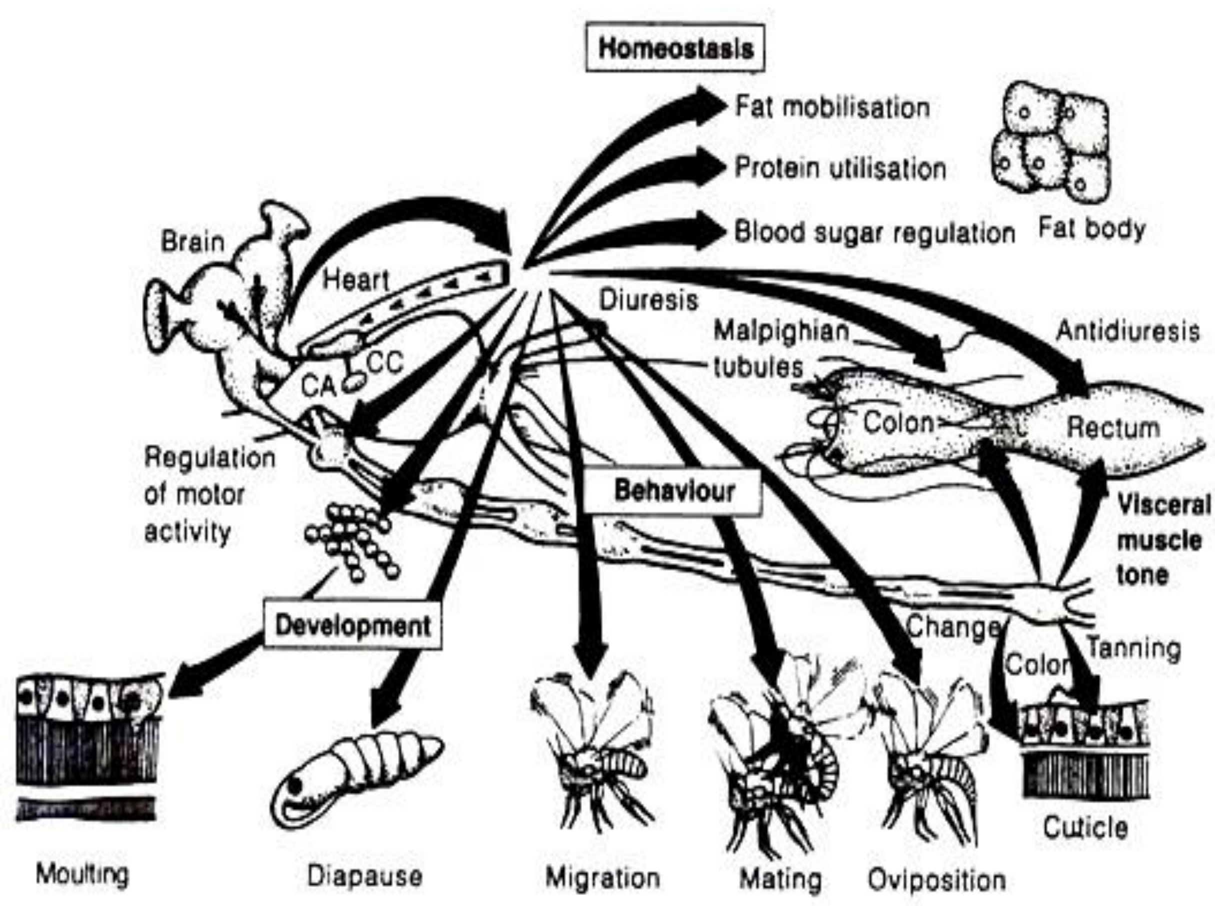

Fig.11.4: Major physiological functions regulated by neurohormones in insects.

11.5 METAMORPHOSIS AND DEVELOPMENT OF INSECTS

(A). Endocrine Control of Growth and Metamorphosis:

- **Moulting:** Emergence from the egg, the immature insects gradually increase in size to reach adults through some mechanisms called moulting. Moulting involves the periodic digestion of old cuticle, secretion of new cuticle (usually with larger surface area than the older one) and shedding of undigested old cuticle. Shedding of undigested old cuticle- is commonly referred to as ecdysis.

  Each developmental stage of the insect itself is called an instar, and the interval of time passed in that instar is referred to as stadium. The whole developmental process by which the first instar immature stage of an insect is transformed into the adult insect is called metamorphosis (Fig.11.5). Hormones required: Brain hormone, Ecdysone, Juvenile hormone.

- **Protocerebrum** secretes brain hormone (BH) or prothoracicotropic hormone (PTTH) or ecdysiotropin which accumulate in the carporaallata and subsequently released into the haemolymph (except in Lepidoptera, in other insects BH is stored in corpora cardiaca). Through the haemolymph, PTTH reach to prothoracic gland and stimulate its secretory activity.
- **Prothoracic glands** secrete α-ecdysone or moulting hormone (MH) which through haemolymph reach the target (epidermis). which initiates the growth and moulting activities of the cells.

- Ecdysone favours the development of adult structures and favours the moulting processes that terminate into successive larval instars.
- The corpora allata secrete juvenile hormone (JH), which promote larval development and inhibit development of adult characteristics
- In fact, JH interacts with MH to stimulate larval maturation during each stage of development. The concentration of JH evidently decreases toward the end of a larval instar, allowing the ecdysone to cause moulting.

- **Ecdysis triggering hormone:** It is the most recent hormone discovered that plays an important role in ecdysis. The 26 aminoacid peptide hormones aresynthesised by the epitracheal glands that are located segmentally in larvae, pupae and adults of *Manduca sexta.* According to Zitnan (1996), this hormone may act upstream from the eclosion hormone in a series of cascade events leading to ecdysis.

- **Bursicon (Tanning hormone):**Bursicon, commonly found in neurohaemal organs associated with the ventral chain ganglia, is suggested to stimulate tanning and sclerotisation of the cuticle following ecdysis.

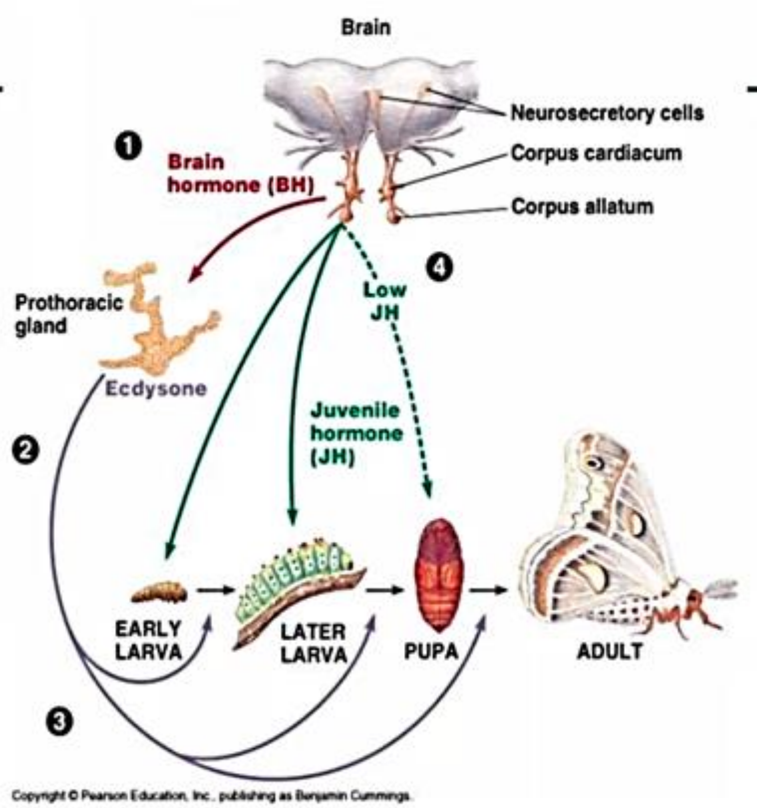

Fig. 11.5: Insect possess hormones that affect metamorphosis

(B). Hormonal control of reproduction:

Like other higher multicellular organisms, reproduction in insects is a complex process. Different stages of reproduction, starting from the production of male and female gametes to oviposition, are seem to be influenced by several hormones.

(i). Spermatogenesis: Ecdysone controls the permeability of the testis walls to the humoral factor differentiating the spermatocytes. Juvenile hormone is shown to have some inhibitory effects on spermatogenesis in many insects.

(ii). Oogenesis: Hormones from corpora allata help in egg maturation through the incorporation of yolk into the oocyte. In addition to secretions from brain cells and corpora allata, ecdysone has been found to be involved in control of oogenesis in female mosquitoes. Following a blood meal, lateral neurosecretory cells secrete egg development neurosecretory hormone, which in turn, induces the ovary to secrete ecdysone. Ecdysone, in turn triggers the synthesis of yolk protein vitellogenin in the fat bodies. Juvenile hormones, secreted by corpora allata, also activate fat body and ovaries.

(iii). Fertilization: In many insects studied, ovulation (the passage of egg from the ovary into the oviduct) and oviposition, (passage of fertilized eggs to the outside, are closely linked. Both these events are affected by some peptides secreted by female accessory glands and neurosecretory products of brain. The process of reproduction involves both the nervous and endocrine systems. The major centers are the neurosecretory cells of brain and the major events are the secretion of juvenile hormone by corpora allata, and either ecdysone production by ecdysial gland in immature insects or ecdysone biosynthesis by the ovary in adult insects. Both hormones act either independently or together in association with nervous system to make reproduction success.

(iv). Vitellogenesis: Vitellogenesis or egg yolk synthesis is also known to depend on JH from the corpora allata. In mosquitoes, juvenile hormone is required for egg development only during the early previtellogenic stages of development of the follicles.

11.6 SUMMARY

Numerous hormonal substances control the physiological, developmental and behavioral activities of insects. These belong to three major chemical classes: steroids (molting hormones), sequiterpenes (juvenile hormones) and polypeptides.Hormones are secreted by specialized glandular tissues in various body regions and by modified neurons (neurosecretory cells).Regulation of hormone titers involves changes in synthesis, release, activation, degradation and excretion.Hormones act upon target tissues via cell membrane and nuclear receptors, eliciting cellular responses and changes in gene expression pattern.

11.7 TERMINAL QUESTIONS AND ANSWERS

Section -A (Very Short Answer Type)

1. Where is brain hormone stored in insect body?
2. Which germ layer gives two prothoracic glands/ecdysial gland?
3. Two small glandular bodies named corpora allata present on either side of
4. ………………..on sides of the oesophagus
5. The word hormone was given by which scientist?
6. Give the synonym of Prothoracicotropic Hormone (PTTH)?
7. What is composition of JH?

Section -B (Objective Type Questions)

1. Endocrine glands of insects which secrete juvenile hormone are____________________.

(a). Corpora allata

(b). Corpora albicans

(c). Corpora myecaena

(d). All of the above

Answer: Corpora allata

2. Hormone Ecdysone is produced by

(a). Corpora cardiac

(b). Prothoracic glands

(c). Corpora allata

(d). Intercerebral gland cells

Answer: Prothoracic glands

3. The juvenile hormone promoting the nymphal characteristics of insects, is produced by

(a). Corpora cardiacum

(b). Corpora albicans

(c). Corpora allatum

(d). Prothoracic glands

Answer: Corpora allata

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UNIT 12: PHEROMONES

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12.1 OBJECTIVES

After studying this module, you shall be able to learn and understand:

v. Basic concept of pheromones
vi. Chemical structure of pheromones
vii. Roles of pheromones in insects
viii. Types of pheromones
ix. Insect behaviour

12.2 INTRODUCTION

In the previous unit, we discussed neuroendocrine system in insects including hormonal control on the physiological, developmental and behavioral activities of insects. Hormones are secreted by specialized glandular tissues in various body regions and by modified neurons (neurosecretory cells).Regulation of hormone titers involves changes in synthesis, release, activation, degradation and excretion.Hormones act upon target tissues via cell membrane and nuclear receptors, eliciting cellular responses and changes in gene expression pattern. In the current unit, we will discuss about insect odours or pheromones. A pheromone is secreted or excreted chemicals that transmit information between individuals of the same species that triggers physiological or behavioural responses in the individual receiving the signal can travel enormous distances, even at low concentrations.

The term "pheromone" was coined by Peter Karlson and Martin Luscher in 1959, based on the Greek word *pherein* (to transport) and hormone (to stimulate). They proposed the term to describe chemical signals from conspecifics that stimulate innate behaviours soon after the German biochemist, Adolf Butenandt had characterized the first such chemical, *bombykol,* a chemically well-characterized pheromone released by the female silkworm to attract mate. It is believed that the first pheromone, *bombykol,* was identified in 1959. Pheromones fall under the broader category of semiochemicals, from the Greek word *semeon* meaning signal or mark, which are simply chemicals through which organisms communicate. Pheromones are also sometimes classified as ectohormones. These chemical messengers are transported outside of the body and affect neurocircuits, including the autonomous nervous system with hormone or cytokine mediated physiological changes, inflammatory signaling, immune system changes and/or behavioural change in the recipient.

12.3 STRUCTURE OF PHEROMONE PRODUCING GLANDS

In most of the insects, pheromones are released by glandular epidermal cells concentrated in discrete areas beneath the cuticle, but, in some species, gland cells are scattered through the epidermis of different parts of the body. In male desert locusts (*Schistocerca gregaria*), for example, class 3 gland cells are scattered over the head, thorax and abdomen. In an immature insect, they are small and restricted to the basal part of the epidermis, but as the insect matures, they enlarge and extend distally towards the cuticle. The cytoplasm in a mature insect, viewed with the electron microscope, contains large numbers of electron-dense granules with numerous clear vesicles close to, and probably discharging into, a terminal cavity. The contents of the cavity are discharged on the surface of the cuticle via a ductule. Similar scattered glands are present in some Heteroptera. In the higher Diptera, the cuticular hydrocarbons forming the sex pheromone are produced by epidermal cells, primarily in the abdomen. Where the secretory cells are aggregated to form a gland, they are usually class 1 gland cells without ducts to the exterior and abutting directly on to the cuticle. The glands are often concealed beneath a fold of cuticle, such as an intersegmental membrane between abdominal segments. They have no reservoir and the pheromone is released directly following its synthesis. In other cases, the glands open into an epidermal invagination which may then serve as a reservoir in which the pheromone accumulates. This is the case with the marking pheromone of social Hymenoptera where larger quantities of pheromone are produced.

Such glands producing pheromones are extensively studied in case of insects:

(a) In Locust:

Mature male locust (*Schistocerca*) through secretion of pheromones accelerate the maturation of other less matured locusts of either sex. This pheromone is secreted by the epidermal cells.

(b) In Lepidoptera:

The males of Lepidoptera (butterflies and moths) produce scent from glands known as androconia, which are located in the wings associated with scales. Androconia have a somewhat elongated structure and terminates in a row of fine processes called fimbriae (Fig. 1A). Pheromones produced by these glands evaporate through these fimbriae.

In queen butterfly, *Danaus gilippus*, pheromone is released by the male and brushed on the female by a pair of brush-like structure called hair pencils. These are present at the tip of the abdomen. On each side of the hind wings of *Amauris* males, there are small scent patches. These patches contain highly modified structures called scent cups (Fig. 1B). These scent cups have a median pore and below the scent cup is present a scent gland. From these scent patches, scent is dispersed by scent brushes associated with genitalia.

In Plaodia, pheromones are secreted from invaginated glands which open on either sides of the last abdominal segment (Fig. 1C). By evagination of this gland, scent is dispersed. Female silk moth emits a sex pheromone called bombykol from a pair of sacs called sacculi lateralis (Fig. 1F). It is found on the last abdominal segment.

(c) In Hymenoptera:

(i) Honey bee:

In honey bee, the pheromones are liberated from two glands — mandibular and Nassanoff's:

1. Mandibular gland:

Mandibular glands are located in the head region. It is a saclike structure and their duct opens at the base of the mandible (Fig. 1D). They are well-developed in the queen and workers but reduced in drones.

2. Nassanoff's gland:

This gland was discovered in 1882 by a Russian biologist, after whom it was named. It is found below the inter-segmental membrane (arthrodial membrane) between the 6th and 7th abdominal segments. This gland is made up of a number of large cells which opens to the exterior by small ducts (Fig. 1E).

(ii) Ants:

Mainly pheromones control the social behaviour of ants as most of their signaling is by means of smell. Pheromones not only control mating in ants but also feeding and exploiting food, recruiting nest mates for battle, warning about enemies, etc.

The total number of scent glands employed are numerous (Fig. 1G a and b) and all these scent glands are meaningful. Different kinds of ants leave pheromone trail from different pheromone- releasing organs. Fox example, trail pheromone is released by *Solenopsis* from its Pavan's gland; in *Myrmica* from poison gland; in *Lasius*from rectal gland.The forager ant, after returning to the nest, uses another pheromone to recruit other ants to come and collect the food. For this purpose,*Myrmica rubra* uses pheromone from its Dufour's gland. If the food source is large and many workers are needed then Solenopsis releases mass-acting pheromones.

The pheromones of ants are released as a volatile liquid. The ants sense pheromones through their antennae and make continual use of both antennae to keep them in the right direction. They steer by balancing the pheromone concentration to the right and left. If the concentration increases to the left, they turn to that direction until both antennae are sensing equal concentrations and thus guide the ants straight down the odour trail.

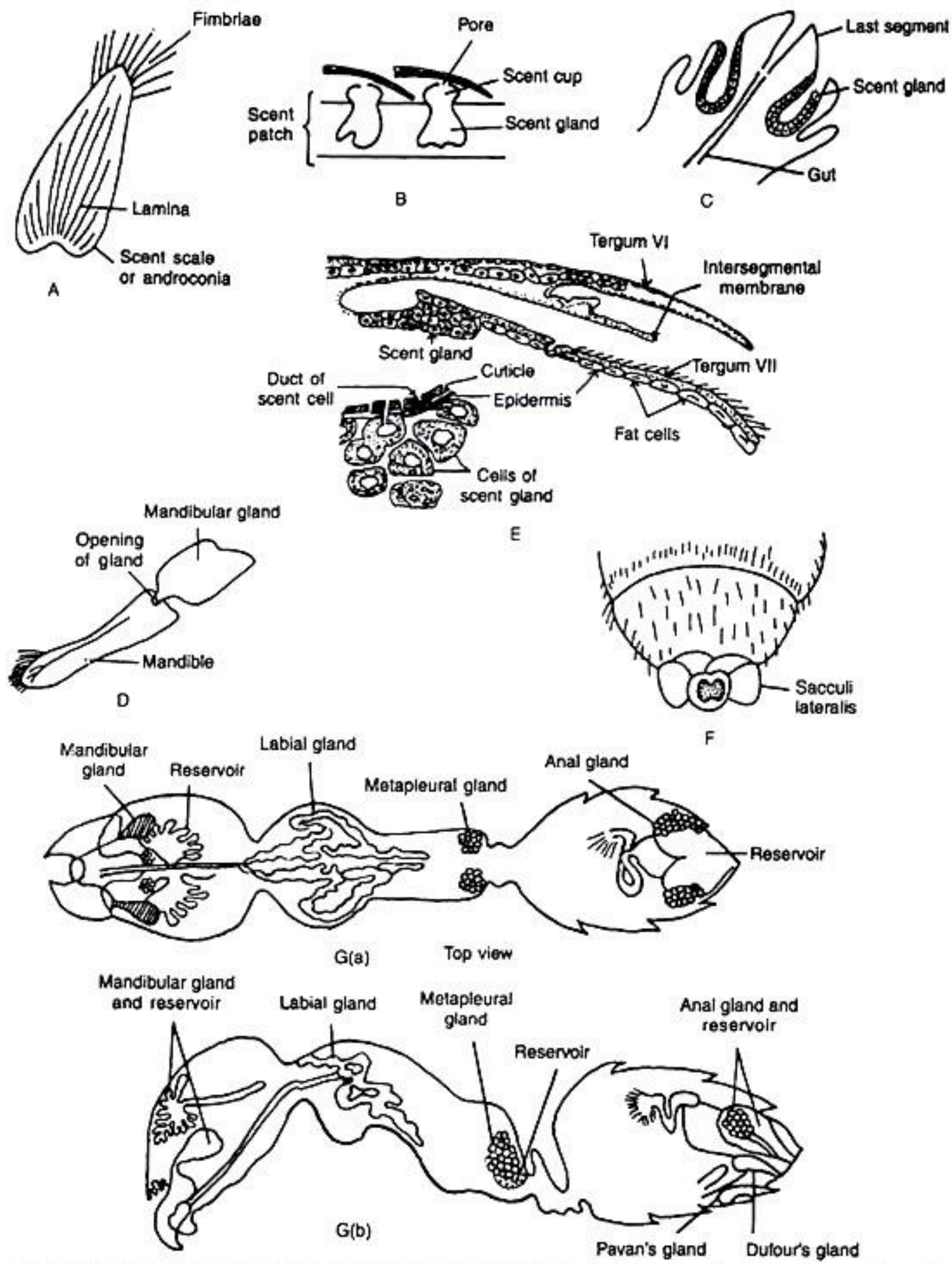

Fig. 12.1: Structures of Pheromones producing glands in insects: A, Androconia of butterflies and moths. B, Scent cups of Amauris males. C. Invaginated scent glands in Plodia. D, Mandibular gland of honey bee. E. Nassanoff's gland of honey bee. F. Sacculi lateralis of silk moth. G (a) and (b) Top and side view of scent producing glands in ants.

12.4 DIFFERENT TYPES OF PHEROMONES

Pheromones are subdivided into several types based on the nature of the interactions between emitters and receivers. Furthermore, releaser pheromones (e.g. alarm pheromone) bring about immediate changes in the behaviour of receivers whereas primer pheromones (e.g. 9-keto-2-decenoic acid or queen honeybee substance) cause relatively slow and long-term physiological changes (Ginzel, 2010; Law and Regnier, 1971).

(a). Aggregation pheromones: These pheromones induce aggregation of insect species at one location is referred to as an aggregation, whether consisting of one sex or both sexes. Male-produced sex attractants have been called aggregation pheromones, because they usually result in the arrival of both sexes at a calling site and increase the density of conspecifics surrounding the pheromone source. Most sex pheromones are produced by the females; only a small percentage of sex attractants are produced by males. Aggregation pheromones have been found in members of the Coleoptera, Collembola, Diptera, Hemiptera, Dictyoptera, and Orthoptera. In recent decades, aggregation pheromones have proven useful in the management of many pests, such as the boll weevil (*Anthonomusgrandis*), the pea and bean weevil (*Sitonalineatus*, and stored product weevils (e.g. *Sitophilus zeamais, Sitophilus granarius*, and *Sitophilus oryzae*). Aggregation pheromones are among the most ecologically selective pest suppression methods. They are non-toxic and effective at very low concentrations.

(b)

Alarmpheromones: Some species release a volatile substance when attacked by a predator that can trigger flight (in aphids) or aggression (in ants, bees, termites) in members of the same species. For example, *Vespula squamosa* use alarm pheromones to alert others to a threat. In *Polistesexclamans*, alarm pheromones are also used as an alert to incoming predators. Pheromones also exist in plants: Certain plants emit alarm pheromones when grazed upon, resulting in tannin production in neighboring plants. These tannins make the plants less appetizing to herbivores.

(c) Epideictic pheromones: These pheromones are different from territory pheromones, when it comes to insects. Females who lay their eggs in these fruits deposit these mysterious substances in the vicinity of their clutch to signal to other females of the same species they should clutch elsewhere. It may be helpful to note that the word epideictic, having to do with display or show (from the Greek *'deixis'*), has a different but related meaning in rhetoric, the human art of persuasion by means of words.

(d) Trailpheromones: Social insects commonly use these types of pheromones. For example, ants mark their paths with pheromones consisting of volatile hydrocarbons. Certain ants lay down an initial trail of pheromones as they return to the nest with food. This trail attracts other ants and serves as a guide. As long as the food source remains available, visiting ants will continuously renew the pheromone trail. The pheromone requires continuous renewal because it evaporates quickly. When the food supply begins to dwindle, the trail-making ceases. Pharaoh ants (*Monomorium pharaonis*) mark trails that no longer lead to food with a repellent pheromone, which causes avoidance behaviour in ants. Repellent trail markers may help ants to undertake more efficient collective exploration. The army ant *Ecitonburchellii* provides an example of using pheromones to mark and maintain foraging paths.

(e) Sexpheromones: These volatile pheromones serve as long-distance signals, emitted by receptive individuals to attract suitable mates. They can be effective over distances of hundreds of meters and possibly even kilometers. In the majority of cases studied, volatile sex pheromones are produced by females to attract conspecific males. However, the situation is sometimes reversed, as seen in some species of weevils and cerambycid beetles, wax moths and phytophagous stink bugs (Hemiptera), where it is the males that produce sex pheromones rather than females. There are also a few cases where both sexes produce pheromones to attract the opposite sex, but during different temporal windows. For example: In the moths *Helicoverpazea* and *Agrotisipsilon*, the bee *Xylocopasonorina* and the butterfly Edith's checkerspot release sex pheromones to attract a mate, and some lepidopterans (moths and butterflies) can detect a potential mate from as far away as 10 km (6.2 mi).

(f) Otherpheromones:

This classification, based on the effects on behavior, remains artificial. Pheromones fill many additional functions.

- Nasonov pheromones (worker bees)
- Royal pheromones (bees)

12.5 CHEMICAL NATURES OF PHEROMONES

The chemical structure of pheromones is widely diverse. Thus, many of them are hydrocarbons, alcohols, esters, epoxides, aldehydes, ketones, lactones, carboxylic acids, isoprenoids, and triacylglycerides. This structural diversity is the key for the pheromone specificity but, in a number of species in Lepidoptera, an appropriate combination of the pheromone components in specific ratio renders the pheromone species-specific. Aggregation pheromones have evolved in various insect groups, but in many cases, the pheromone components generally consist of multiple compounds mainly including volatile aldehydes, alcohols, esters, ketones, aromatic compounds, and terpenoids.

For example, the adult locusts use aromatic compounds, and nymphal locusts use volatile aldehydes, volatile carboxylic acids, aromatic compounds, and indol.Stink bugs use sesquiterpenoids or esters, thrips use a blend of esters, and bed bugs use a mixture of volatile sulfur-containing compounds, aldehydes and a ketone. In bees and wasps, *Colletes* bees use volatile terpenoids, a wood wasp uses a volatile alcohol, and parasitoid wasps use volatile ketones and spiroacetals. Moths use volatile ketones, aldehydes, monoterpene, and alcohols. Beetles use various types of compounds as aggregation pheromones depending on taxonomic groups; red flour beetles use a volatile aldehyde, bark beetles mainly use terpenoids, and longhorn beetles use mixtures of volatile ketones, alcohols, aromatic compounds, and terpenoids. On the other hand, some insects use not only volatile compounds but also non-volatile compounds as aggregation pheromones. For example, *Drosophila* flies use esters, ketones, and long-chain hydrocarbons. Although German cockroach is the first species that the presence of aggregation pheromone is suggested, the identification of this pheromone remained to be discussed. But a recent study revealed that German cockroaches use volatile carboxylic acid or non-volatile fatty acids as aggregation agents, and the components of the agent vary a little depending on the cockroach populations. In termites, our results demonstrated that *R. speratus* workers use an aromatic compound, long-chain hydrocarbons, and fatty acids for their aggregation pheromone. Considering that the compounds used for insect pheromones (alcohols, aldehydes, esters, hydrocarbons, carboxylic acids, and terpenes) are generally biosynthesized via lipid metabolic pathways, it is suggested that basic components of insect aggregation pheromones are synthesized from lipid derivatives, and that adding idiosyncratic compounds (e.g., compounds having unique structures, other compound groups such as aromatic compounds) to a pre-existing aggregation pheromone may contribute to differentiating pheromone components from those of other species. Cuticular hydrocarbons (CHCs) play an important role in nestmate and caste recognition in social insects. The CHCs of worker *Reticulitermes* termites include straight (or branched) alkanes and alkenes with >20 carbon molecules; these may act as cues in species and nestmate recognition, as demonstrated in ants. The GC-MS analyses detected straight-chain and methyl-branched alkanes bearing 23–31 carbon molecules from the extracts of *R. speratus* workers; C25 and C27 were the two most abundant compounds among those found in CHCs among workers.

12.6 IMPORTANCE OF PHEROMONES IN INSECT ACTIVITY

Currently, pheromones and other semiochemicals are being used to monitor and control pests in millions of hectares of land (Witzgallet al., 2010). Highly relevant for IPM programmes of tephritidfruitflies is the use of parapheromones. These are chemical compounds of anthropogenic origin, not known to exist in nature but are structurally related to natural pheromone components, that in some way affect physiologically or behaviourally the insect pheromone communication system, eliciting a similar response to that of a true pheromone (Renou and Guerrero, 2000). For example, males of many *Bactrocera* and *Dacus* species are strongly attracted to specific chemical compounds, which either occur naturally in plants (e.g. methyl eugenol) or are synthetic analogues of plant-borne substances (e.g. cue lure)

(Cunningham, 1989; Fletcher, 1987). Parapheromones are very powerful lures used in current programmes aimed at detecting, monitoring, and controlling (through the Male Annihilation Technique) invasive tephritid pests (Vargas et al., 2008).

Pheromones in pest management:

Pheromones are used for:

– Monitoring

– Trapping-out

– Attract-and-kill

– Mating disruption/confusion

– Alarm and oviposition deterrentthe branches of a perimeter-row apple tree with grandisoic acid (aggregation pheromone) and benzaldehyde (synthetic fruit volatile) to attract plum curculio adults, monitoring then focuses on sampling just a few fruit from that perimeter-row odor-baited trap tree.

(i). Pheromones for monitoring: Males often can be attracted by confining virgin females in cage. However, pheromone ID and synthesis is quite advanced, and most chemicals can be identified and synthesized. Synthetic lures often enclosed or impregnated in rubber or polyethylene, which provides gradual release. Trap is often a simple roof structure with sticky bottom to entrap insects, or roof over funnel with container for retaining insects that fall into funnel. Ability to attract large number of insects has encouraged many attempts to reduce populationdensities with combination of sex pheromones and traps. Even where aggregation pheromones, or sex plus food-based lures used, population suppression often inadequate. Highly efficient traps needed.

Fig.12.5: Pheromone trap for mass trapping of moths

Fig. 12.4: Funnel Trap with Brinjal Lure.

(ii). Attract and kill systems: Pheromone or pheromone-like chemical used to bring insect into contact with insecticide. Treatment sprayed into crop, reduced area of crop, or non-crop area. Example: methyl eugenol for Oriental fruit fly.

(iii). Mating disruption/confusion: The basic concept is to saturate an area with pheromone, preventing males from finding females. Exact mechanism not known, perhaps:

– Camouflage of natural by synthetic pheromones

– Synthetic pheromone out-competes natural

– Synthetic pheromone acts as antagonist

– Breakdown of sensory neurons

– Insects habituate to chemical, no longer respond.

(iv). Pheromones other than sex pheromones: Oviposition deterrent or oviposition marking pheromones are fairly common, and have been shown experimentally to be effective at reducing damage by reducing egg-laying. Alarm pheromones occur in several orders, but best known in aphids - (E) beta-farnesene, released from cornicles, causes other aphids to disperse. Can be used to increase likelihood of contacting insecticide.

12.7 SUMMARY

Insects communicate with each other and obtain information about their environment with info-chemicals.Insects use info-chemicals called pheromones for intraspecific communication, and these are classified according to their function (e.g., sex pheromone, trail pheromone or alarm pheromone).A wide variety of pheromones are used by social insects to mediate all aspects of colony organization and function.Interspecific interactions are modulated by chemical cues known as allelochemicals. These are classified as allomones if they benefit the emitter, kairomones if beneficial to the receiver or synomones if they are beneficial to both emitter and receiver.Chemical signals of one species (e.g., sex pheromones) are often exploited as kairomones by predators or parasites for prey location. In extreme cases predators actually mimic the pheromones of their hosts to attract them as prey, or as chemical camouflage to avoid detection. This is known as chemical mimicry.Insects can produce a large number of unique signals from a relatively small pool of chemicals by using blends of different compounds, using different ratios of the same set of compounds and by manipulating the stereochemistry of pheromone components.

12.8 TERMINAL QUESTIONS AND ANSWERS

(A): Long Answer Type Questions:

a) Can you distinguish between semiochemicals, pheromones, and allelochemicals?

b) Can you name 3 types of pheromones? Of allelochemicals?

c) Describe the major approaches to using pheromones in pest management.

d) Which are used commercially? What is the major (most frequent use?)

e) What are some of the current and potential constraints on use of pheromones for pest management?

(B): Multiple Type Questions:

1. The pheromone coated paper strips in the confusion technique are thrown over an area to

(a) Confuse males so that they are unable to locate females

(b) Repel insects from a region

(c) Confuse females so that they are unable to locate males

(d) Attract insects and kill them

Answer: (a) confuse males so that they are unable to locate females

2. Chemicals that are released by organisms as a means of communication between members of the same species are:

(a). Pheromones

(b). Releaser Pheromones

(c) . Primer Pheromones

(d). All of the above

Answer: All of the above

3. Which one of the following is called intra-specific chemical messenger?

(a). Pheromone

(b) Prostaglandins

(c) corticotropic

(d) catecholamines

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UNIT 13: EMBRYOLOGY

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UNIT 13.1: OBJECTIVES

Following completion of this module, you should be able to understand:

- Basics of insect Embryology
- Different formation of insect embryoes
- Structure of insect egg
- Type of larvae
- Type of pupae
- Reproduction in insects

UNIT 13.2: INTRODUCTION

In the previous unit, we discussed the importance of insect odours, which are commonly known as pheromones. The insects communicate and obtain information about their environment with info-chemicals or pheromones for intraspecific communication, and these are classified according to their function (e.g., sex pheromone, trail pheromone or alarm pheromone).Interspecific interactions are modulated by chemical cues known as allelochemicals. In this unit, we discuss on the embryology of insects. Embryology is the branch of biology which deals with the growth and development of an embryo of an organism, commencing with the union of male and female gametes. Embryology includes the development of the fertilized egg and embryo and the growth of the organ system. A scientific field known as embryology studies how embryos are formed, grow, and develop. It focuses on the prenatal stage of development, which starts with the formation of gametes, fertilization, zygote formation, embryo and foetus growth, and ends with the birth of a new organism.

The initial stage of development is the embryonic stage, which starts with the fertilized egg or the first cleavage stage, and concludes with the animal's hatching or birth. Even among the mostly oviparous Eutracheata, the transition from one stage to the next occurs gradually. For instance, the eggshell, or chorion, is broken before the embryo is fully developed in the Myriapoda, Collembola, and certain other insects, yet in other instances a fully-grown insect larva may lie latent within the eggshell for a period of several months before emerging. The second stage, often known as adolescence, is a time of growth and maturation for the reproductive organs. Many creatures undergo a period of noticeable change in their outer appearance during this time, especially amphibians and hemi- and holometabolous insects. Known as the "postembryonic stage" in insects, it is typically much longer in this context and can persist for weeks, months, or even years. The third phase is the one of sexual development and childbearing. In vertebrates and certain other invertebrates, it may last for many years, but in the Eutracheata, it often lasts only a few hours in the case of the Ephemeridae. Senescence, sometimes known as a stage of degeneration and death, is the last stage. In terms of phylogenetically, it means nothing. We are here concerned with the first of these stages, the embryonic stage of development.

UNIT 13.3: EARLY EMBRYONIC DEVELOPMENT

The position of the future embryo is clearly related to the distinction between the anterior and posterior poles found in the eggs of the majority of insects. The placement of the eggs within the ovarioles ensures that each egg's cephalic pole faces the parent's head and that its dorsal and ventral aspects match those of the parent and upcoming embryo.

As soon as the egg is laid after fertilization, the zygote nucleus divides and the daughter nuclei go to the edge of the egg to create a layer of cells called the blastoderm that surrounds the yolk. To create the germ band, which is where the embryo grows, a portion of this cell layer thickens. Gastrulation then occurs, causing the formation of an inner layer of cells beneath the germ band. The process of gastrulation varies in its specifics, making it difficult to directly compare it to gastrulation in other animals. Extra-embryonic membranes that separate the embryo from the egg's surface when it moves more or less extensively inside the yolk eventually dissolve and vanish. The yolk is now encased within the bodywall, thanks to these motions, which also bring the embryo to its final position. The body wall, the tracheal system, the stomodeum, and the proctodeum are all formed by the ectoderm. The neurological system and the sensory organs are also ectodermal in origin. Coelomic sacs may initially form in the mesoderm, but they disintegrate to create muscles, the circulatory system, and the reproductive system. Early in development, sometimes only after a few nuclear divisions, the germ cells from which the sex cells ultimately derive differentiate.

UNIT 13.4: STRUCTURE OF EGGS

Life begins as an independent egg in the majority of insects. Ovarian reproduction is the term for this process. Each egg is created within the female's genital system and subsequently expelled from her body through an ovipositor, a part of her external genitalia that resembles a tube, saw, or blade. The process of the female's body producing eggs is known as öogenesis, and the act of laying the eggs is known as oviposition. Each insect species produces eggs that are spherical, ovate, conical, sausage-shaped, barrel-shaped, or torpedo-shaped, as well as genetically distinct and frequently physically unusual. In spite of this, each egg only contains one living cell, the female gamete, regardless of its size or shape.

Insect eggs are frequently larger than the size of the females who lay them because they frequently contain a large amount of yolk. Exopterygota eggs are often regarded as being larger and having more yolk than Endopterygota eggs. However, factors other than the ovariole type also have an impact on egg size. Lepidoptera from temperate locations have larger eggs than those from other stages of overwintering, and species that feed on woody plants have larger eggs than those that feed on herbaceous plants. As they get older, at least some butterfly females produce smaller eggs, while females of the cornborer moth, *Ostrinia*, produce smaller eggs when they are malnourished. The Tachinidae share this trait with the parasitic Hymenoptera, which lay their eggs inside of their hosts (Diptera). Insect eggs come in a wide range of shapes. They are typically sausage-shaped, like many Orthoptera and Hymenoptera, but they can also be conical, like *Pieris*, or rounded, like many moths and Heteroptera. The eggs of many parasitic Hymenoptera have an extension at one end called a pedicel, but the eggs of Nepidae and other Diptera have respiratory horns. Hymenoptera's *Encyrtus* eggs are distinctive in that they are made up of two bladders joined by a tube. The proximal bladder is lost during oviposition as the contents of the egg travel from it to the distal bladder.

(a). Egg Structure

A hard shell, known as the chorion (ch), protects the oval egg, which is slightly flattened on the dorsal side (Fig. 13.1). The thin vitelline membrane lies beneath the chorion. Its contents are made up of an internal protoplasmic reticulum (r) in the meshes where the food jelly is retained, as well as a thin layer of protoplasm (pr) at the surface (periplasm). In the middle or close by is the egg nucleus (nu). The vitelline envelope and the chorion combine to produce the egg's shell, which is made up of some cytoplasm and a significant amount of yolk.

(b).The cytoplasm

The egg's nucleus is positioned in the centre and surrounded by cytoplasm. The cytoplasm of the egg develops a periplasmic boundary layer at the time of oviposition, and an irregular reticulum within the yolk. In insects with meroistic ovarioles compared to those with panoistic ovarioles, the cytoplasm (euplasm) is significantly more extensive, suggesting the higher contribution of the germ line genome to the egg. The zygote nucleus often sits in the back.

(c).Vitelline envelope

A protein-rich covering that envelops the oocyte is called the vitelline envelope. In other scene, two shells protect the eggs: a thick outer shell known as the chorion and a softer inner shell known as the vitelline membrane. Although it is frequently referred to as the vitelline membrane, it is best to reserve the term "membrane" for cellular structures as the vitelline envelope is extracellular. It is typically between one and two metres thick, but in the parasitic Hymenoptera, it is much thinner—150 nanometers in *Habrobracon* and *Nasonia*, and nine metres in *Sympetrum*, the damselfly. It is not always consistent in structure throughout the whole surface of the oocyte and may vary in thickness in different areas of the egg. For instance, in *Drosophila*, it has openings where the chorion splits after hatching, and in *Lytta*, a beetle, it is pierced beneath the micropyles.

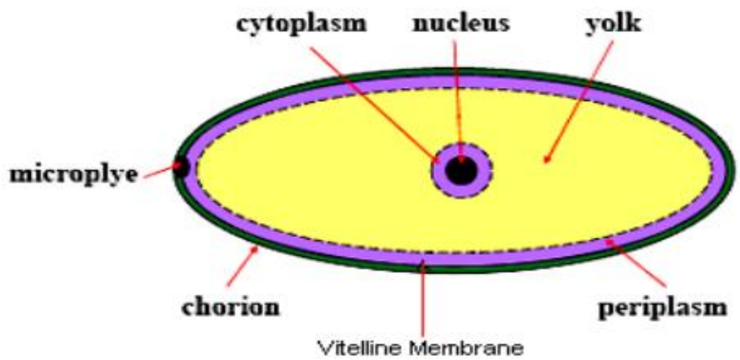

Fig.13.1: Egg structure.

(d).Chorion: The exterior of an insect's egg is called the chorion. A waxy layer that stops water loss can be one of the many layers that make up the chorion. Insects can lay their eggs singly, in large groups, or even by injecting them into other organisms.

The chorion or eggshell is a tough, non-chitinous, protective covering, secreted by the cells lining the ovarian follicles. The chorion is of two layers, a thick inner endochorion and an extremely thin outer exochorion, which is composed of a chemical substance, scleroprotein, which is similar to the cuticulin of the insect epicuticle, and is also sometimes called chorionin. Usually, some part of the chorion contains extensive airspaces with chorionic struts (Fig. 13.2).

While the egg is in the ovary, the follicle cells create the intricate structure known as the chorion. Eggs from parasitic Hymenoptera have a thickness of less than one micron, while some orthopteran and lepidopteran eggs have a thickness of over 50 microns. The chorions of even closely related species can vary in thickness. For instance, the chorion of *Bombyx* in silkmoths is around 25 m thick, whereas that of *Hyalophora* is 55 m thick. It is assumed that these variations have ecological importance. Many insects have an innermost layer of the chorion that is crystalline and less than one micron thick. This layer is outside of any wax layer and contains proteins that are stabilized by disulfide or dityrosine linkages. The chorion's outer surface is typically sculpted, frequently in a pattern that is primarily hexagonal and reflects the geometries of the follicle cells that secrete it.

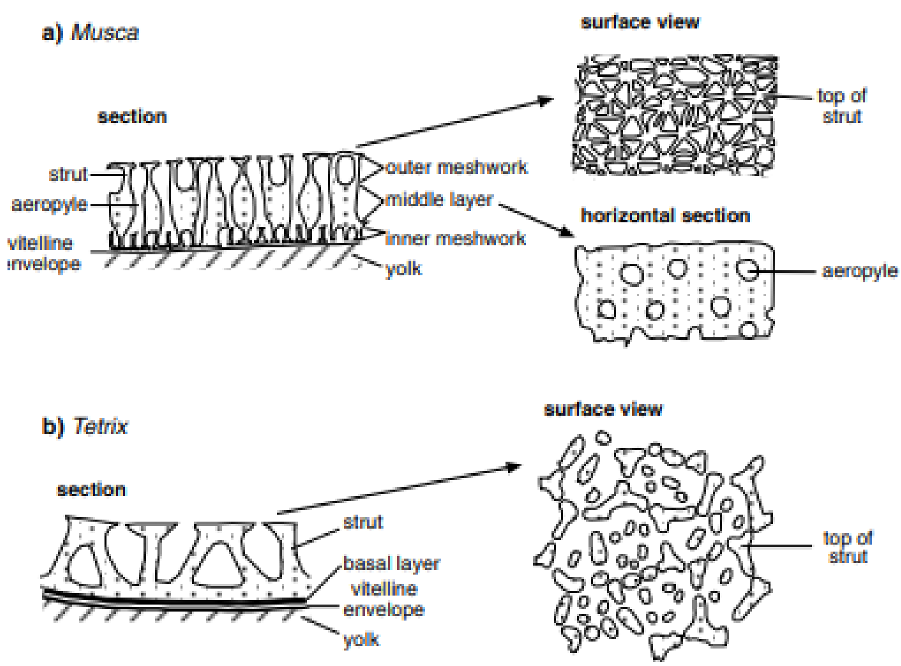

Fig. 13.2: Airspaces in the chorion. (a) A chorion in which the air-filled inner meshwork connects with the exterior through a limited number of aeropyles [Musca (Diptera)] (after Hinton,1960). (b) A chorion in which extensive airspaces extend through its thickness.Figure Source: The Insects Structure and Function, 4th edition by R.F. Chapman

(e). Micropyles

Since the chorion is established in the ovary, some preparation is required to permit the entry of sperm later. Micropyles, funnel-shaped pores that flow directly through the chorion and are typically found close to the anterior pole of the egg, are one way that this manifest itself. The pores have a diameter of 1-2 metres and frequently have a larger funnel at the chorion's surface. Under the micropyles, the vitelline envelope is also altered. Acrididae (grasshoppers) typically have 30 or 40 micropyles grouped in a ring at the posterior end of the egg, but most dipteran eggs only have a single terminal micropyle. The micropylar apertures can occasionally be elevated above the egg's surface and linked to aeropyles. The micropylar canal travels through the chorion and the process, and it is enclosed by an open reticulum that contains airspaces.

(f). Fertilization:

In general, fertilization occurs after the eggshell has been produced in insects. The sperms that the male had previously placed in the spermatheca (or, in some cases, the bursa) are received by the egg as it passes through the opening of the spermathecal duct by way of the micropyles as it descends from the ovary. Although polyspermy—in which multiple sperms penetrate the micropyles—is the norm for insects, monospermy has been observed in parasitic Hymenoptera and some other insects. The extra sperms that are produced during polyspermy deteriorate in the yolk. In *Drosophila* eggs, extra sperm degrade and hardly ever produce mitotic figures.

It's common to see the generation of male (sperm) and female (ovum) gametes as the initial stage of insect development. The second stage of development is the fusion of gametes (spermatozoon and ovum), which results in a diploid zygote with the capacity to develop into a whole organism. This process is triggered by the fertilization of ovum with sperm. Most insect sperm can survive in the spermatheca for months to years. When the eggs are going to be laid and while they move through the oviduct, fertilization takes place. The micropyle allows the sperm to reach the eggs. A number of sperms enter the eggs, and one of them fertilizes the eggs to create a zygote while the other sperms degenerate.

Rarely are fertilization membranes addressed in relation to insects. In the silkworm, after forced parthenogenesis, the first brood of two-brooded stocks, but not the second brood or single-brooded stocks, a robust fertilization membrane separates from the egg. This variation's significance is unknown.

UNIT 13.5: MATURATION

In an insect egg, maturation starts as soon as the sperm enters, causing the creation of the female pronucleus and the change of the sperm's head into a male pronucleus to occur simultaneously. Despite the possibility of several sperm entering the egg, only one male pronucleus fuses with the female pronucleus to create the fusion nucleus (**synkaryon**).

Asters are absent from the maturation spindles, although centrosomes can be present, as in *Miastor*, or lacking, as in *Apis* and Lepidoptera. The first polar body may undergo a second mitotic division, resulting in the formation of three polar bodies. However, in certain instances, such as in *Pseudococcuscitri*, the first polar body either does not undergo a second division or divides just partially. With *P. citri*, the haploid and diploid chromosome groups of the first and second polar bodies combine to form a triploid group that divides mitotically, producing enormous cells with nuclei that are surrounded by cytoplasm that will eventually associate with the symbionts of the egg. When the process has been completed, the giant cells are known as "**mycetocytes**."

Chromatin elimination may occur in the eggs of several species of Lepidoptera, Diptera, and other life forms during the first maturation division. The elimination occurs in the shape of an equatorial disc, with the quantity eliminated being variable and the amount remaining in the daughter remaining constant.

The location of the maturation divisions in the egg is not fixed. It is not far from the anterior pole in *Simulium*, certain other Diptera, and *Diacrisia*; below the midpoint on the dorsal side in *Melophagus*; and midventral in *Pteronarcys*. It has been noted that it is unclear whether or not the point of entry and course of the sperm bear any relationship to the origin of the orientation of the embryo because they are likely constant in any one species due to the location of the micropyle. The only instances when any aspect of fertilization is believed to affect development, aside from starting the maturation divisions' completion, are in incompletely determined eggs. Immediately following the onset of cleavage, the visible zonation of the ant egg's cortical layer is induced, as is a comparable but imperceptible determination in the beetle egg. It is unknown how this activation of the activation centre occurs or whether the entry of the sperm, the fusion of the pronuclei, or another mechanism is to blame.

UNIT 13.6: STRUCTURE OF EGGS

The repeated mitotic divisions of a fertilized ovum zygote are known as cleavage. The zygote nucleus of an egg begins to divide after fertilization. After fertilization, the sperm and egg nuclei fuse at the egg's periphery to generate the diploid fused-nucleus (zygote), which then moves into the egg's centre. The zygote nucleus repeatedly divides, resulting in the division of one cell into two daughter cells known as blastomeres, which subsequently cleave into four; these cleave into eight, and so on, which creates a lot of daughter nuclei in the end. The daughter nuclei are then accompanied by a hollow mass of cytoplasm, known as energids or cleavage cells, which are nucleocytoplasmic units.

Despite the fact that most arthropod eggs only go through superficial cleavage, there are a few exceptions. The groups listed below may be recognised-

1. **Eggs with a Purely Superficial Cleavage-** The fusion nucleus divides into daughter cells which by repeated division and migration to the periphery give rise to a layer of cells or primary epithelium commonly known as the "blastoderm." This type occurs with eggs rich in yolk, but it also occurs exceptionally in certain cases where there is a deficiency in yolk as in the eggs of aphids, some Platygastridae, and Hemimerus.

2. **Eggs with a Combination Cleavage-** Combination cleavage that is total at first and later becomes superficial has been observed in the group Collembola, and even among them *Anurophonis* and *Tetrodontophora* undergo a purely superficial cleavage. The combination type which the entire egg mass divides until it forms the 32- or 64-cell stage, each nucleus surrounded by a protoplasmic envelope which in turn lies in the center of a yolk spherule. The nucleated cell-like bodies now migrate, first to the surface of the yolk spherules and then to the periphery of the egg, leaving the yolk spherules in the center, thus forming the blastula. The early development of *Anuridamaritima* does not essentially differ. In the genus *Tomocerus* (*Macrotoma*) the development starts with the division of the nucleus, but it is not until the third or fourth division that the yolk also begins to divide. At the 32-cell stage the

yolk-cell walls disappear, and the yolk nuclei pass to the periphery of the egg, where through tangential division of the nuclei the blastoderm is completed. In the forms mentioned cleavage is equal; but in *Achorutesarmatus,* according to Uzel, an unequal cleavage takes place with the formation of micro- and macromeres. A possible case of combination cleavage has been briefly described by Strindberg for an ant of the genus Azteca.

3. **Eggs with Purely Total Cleavage-** Purely total cleavage occurs in the eggs of several parasitic Hymenoptera and is associated in most cases with polyembryony.

13.7: BLASTOKINESIS

The energids move and migrate towards the periphery (periplasm) of the egg and arrange in a layer of circlet within the yolk. The energids may undergo further, one or more mitotic divisions and retain the distinct cell walls and subsequently form a layer of cells, called the blastoderm. The blastoderm, in true sense, is the primary germinal epithelium. It lies just beneath the vitelline membrane.

The blastoderm consists of a layer of columnar cells on the ventral side of the egg and a flattened epithelial stratum over the remainder. Those cleavage cells which remain in the yolk form the primary yolk cells or vitellophages, which become augmented by secondary yolk cells derived by the immigration of cells from the blastoderm. In some cases, it appears that the yolk cells are only derived from the latter source. Among several orders of insects, notably Orthoptera, Lepidoptera and Coleoptera, the yolk undergoes secondary cleavage, becoming thereby divided into polyhedral masses each of which contains one or more yolk nuclei. The function of the yolk cells is to liquefy the yolk and bring about its assimilation.

Differentiation of the Blastoderm - Irrespective of whether the newly formed blastoderm is quite uniform or already shows signs of precocious differentiation, the next major stage of development leads to a condition in which some of the blastoderm forms a thin layer of extra-embryonic ectoderm covering part of the yolk surface, while the remainder of the blastoderm develops into a thicker, though still one-layered, embryonic primordium. It is the embryonic primordium that gives rise to most of the tissues and organs of the later embryo and it varies considerably in size and shape. In Diplura and Colembola, it occupies much of the surface of the yolk mass; in the Thysanura and lower Pterygota it is a thin layer restricted to a relatively small posteroventral region, while in the Hemipteroid orders and the Endopterygota, it is thicker and more extensive, especially in the *Cyclorrhaphan* Diptera. The cells of the embryonic primordium show little histological differentiation, but the subsequent developmental fate of its various regions is remarkably constant within the Pterygota.

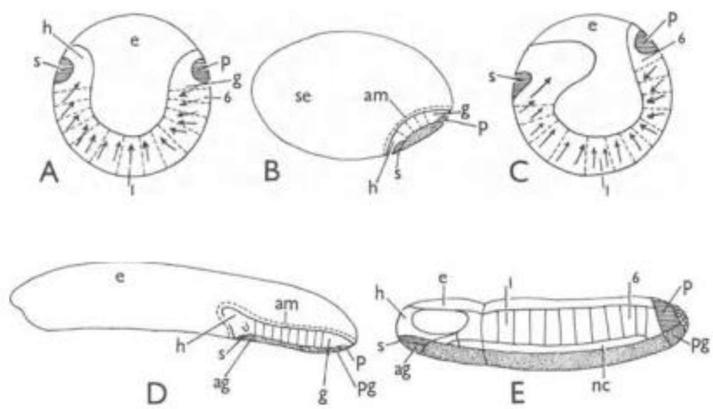

Fig.13.3: Fate maps of the insect blastoderm (after Anderson, 1973). A- Diplura; B-Thysanura; C-Collembola; D- Odonata (Platycnemis); E- Diptera (Dacus).

The various 'presumptive areas' of the differentiated blastoderm can therefore be marked out on 'fate maps' which show that the embryonic primordium comprises five main regions (Fig. 13.3) : (i) a narrow mid-ventral band of presumptive mesoderm cells, at each end of which lie (ii) the small presumptive areas of the anterior and posterior mid gut; (iii) and (iv) the presumptive stomodaeum and proctodaeum, lying respectively in front of and behind the corresponding mid gut areas; (v) a pair of latero-ventral bands of presumptive ectoderm, which border the other regions and are joined anteriorly in front of the presumptive stomodaeum, where they take the form of broad head-lobes. In the few Apterygota that have been adequately studied, the mid gut is formed from vitello phages so that presumptive mid gut areas are not found in the blastoderm. The Thysanura have a presumptive mesoderm area like that of the Pterygota, but in the Collembola and Diplura the mesoderm arises diffusely over the whole of the presumptive ectoderm area

UNIT 13.8: STRUCTURE OF EGGS

(a). Formation of Germ Layers

The blastoderm of most insects is initially a uniform layer of cuboid cells all over the yolk. Subsequently, it becomes thicker in the ventral region of the egg due to the aggregation of the cells so that they become columnar. This thickening is the embryonic primordium, or germ band. It develops into the future embryo, while the rest of the blastoderm remains extra-embryonic. In some Lepidoptera, the blastoderm is differentiated into germ band and extra-embryonic tissue from the time of its first appearance and in some other insects, such as *Mallophaga* and *Apis*, the whole blastoderm is thick initially but subsequently becomes thinner except for the germ band. In eggs containing little cytoplasm, like those of most insects with panoistic ovarioles, the germ band is a small disc or streak of tissue over the posterior end of the egg **(Fig. 13.4).** In insects with polytrophic ovarioles, it is more extensive and, in dipteran eggs, which contain a relatively small amount of yolk, the germ band is formed from most of the blastoderm and there is very little extra-embryonic tissue. Where the germ band is short relative to the whole egg, embryonic development usually involves the differentiation of additional tissue posteriorly. Where the germ band is large, all the parts of the larval body are represented from the outset. The germ band is differentiated into a broad head region, the protocephalon, and a narrow 'tail',the protocorm and in a typical hemimetabolous insect,the midventral cells of the germ band are the presumptive mesoderm and midgut. The presumptive stomodeum and proctodeum lie at either end of this. In higher Diptera and some Lepidoptera and Hymenoptera, the fate of the different parts of the egg is much more precisely determined, but the same general arrangement of presumptive areas exists. In holometabolous insects, these presumptive areas relate to the development of larval tissues, but, where most or all of the adult tissue develops from imaginal discs (section 15.3.2.2),these areas may also be determined at a very early stage of embryonic development.

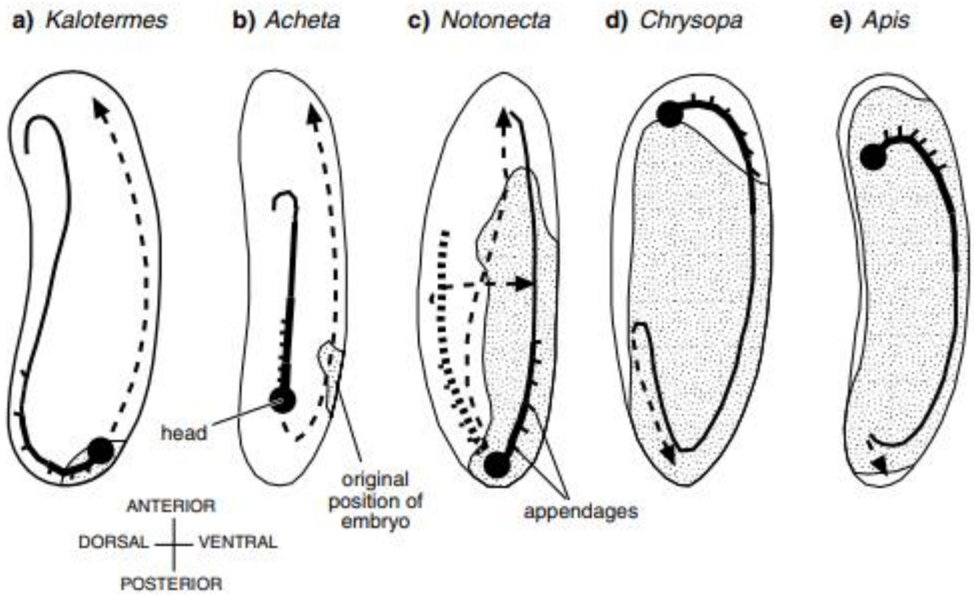

Fig.13. 4: Diagram showing the position of the germ band (stippled), the position of the embryo before blastokinesis (solid black,showing the protocephalon and gnathal and thoracic appendages),and movement of the embryo at katatrepsis. In all cases the embryo finally comes to lie on the ventral surface of the egg with its head at the anterior pole. (a) termite (Kalotermes, Isoptera); (b) Cricket (Acheta, Orthoptera); (c) backswimmer. The embryo first develops on the dorsal side of the egg and moves to the ventral side (transverse arrow) before reversing its position in the egg (Notonecta, Hemiptera); (d) green lacewing (Chrysopa, Neuroptera); (e) honeybee (Apis, Hymenoptera). (Source: The Insects Structure and Function, 4th edition by R.F. Chapman)

(b). Formation of Segmentation:

(i). Mesoderm and body cavities

The mesoderm is derived from the inner layer of the germ band which forms two lateral strands running the length of the body and joined across the midline by a thin sheet of cells. In the lower orders, the lateral strands become segmented and the somites separate off from each other, but in Lepidoptera and Hymenoptera the somites remain connected together. Amongst the Cyclorrhapha, there is a tendency for the mesoderm to remain unsegmented. In *Dacus*, for example, the strands of mesoderm only become segmented as they differentiate into the definitive structures. The mesoderm in the protocephalon arises in situ in the lower orders, but moves forwards from a postoral position in the more advanced groups.

(ii). Alimentary canal: The foregut and hindgut arise early in development as ectodermal invaginations, the stomodeum and proctodeum. These invaginations carry the anterior and posterior rudiments of the midgut into the embryo. These rudiments then extend towards each other forming two longitudinal strands of tissue beneath the yolk and above the visceral mesoderm. From these strands, midgut tissue spreads out over the surface of the yolk, eventually completely enclosing it.

(iii).Reproductive system: The germ cells, from which sperm and oocytes are ultimately produced, become separated from the somatic cells very early in development. This early separation of the germ line results in a very direct cell lineage from the gametes of one generation to the gametes of the next, in isolation from the structural cells of the body. This presumably helps ensure the integrity of the genetic system by reducing the possibility of DNA replication errors.

(iv). The Nervous System: The beginnings of the central nervous system appear as a pair of longitudinal neural ridges of the ectoderm of the germband, about the time when the latter becomes segmented. They begin at the sides of the stomodaeum, and continue backwards until they unite behind the proctodaeum. These ridges are separated by a median furrow - the neural groove. A chain of cells forming the median cord is separated from the ectoderm lining the neural groove. The ectoderm cells forming the neural ridges become segregated into two layers - an outer thin layer of dermatoblasts which forms the ventral body-wall and an inner layer of neuroblasts which forms the nervous tissue. When the embryonic appendages start to appear, the neural ridges become segmented into definite swellings at their bases, and each pair of swellings constitutes a neuromere. The intrasegmental portions of the median cord and neural ridges give rise to the definitive ganglia, while the intersegmental portions of the ridges form the connectives.

(v).The Tracheal System: Shortly after the appearance of the neuromeres, the tracheae appear as ectodermal invaginations lying just outside the bases of the appendages. As a rule, ten pairs are developed, and they occur on the last two thoracic and first eight abdominal segments. In a few species embryonic tracheal invaginations develop on the prothorax or 9th and l0th abdominal segments but close before hatching.

(vi). The Salivary Glands: These appear as a pair of ectodermal ingrowths of the labial segment. As they increase in depth their apertures approximate, and become drawn into the preoral food cavity where they finally open by a median pore into the salivarium.

(vii).The Body-wall: The body-wall is directly derived from the superficial ectoderm, as are also the invaginations that give rise to the apodemes, temtorium and other endoskeletal structures. The sensory neurons and integumentary components of the sense organs are also formed from the general ectodermal surface of the embryo and the corpora allata arise as invaginations of the cephalic ectoderm.

(viii). The Body-cavity and Dorsal Vessel: The permanent body-cavity begins as a space - the epineural sinus, which is mainly produced by the separation of the yolk from the embryo over the region of the ventral nerve cord. The process of separation extends laterally, and in some insects the walls of the coelom sacs are stated to break through in such a manner that their cavities become confluent, both with one another and with the epineural sinus; in other cases, however, the coelomic cavities are known not to unite with the epineural sinus. The developing haemocoele extends upwards along with the mesoderm, on either side, until the formation of the body-cavity is completed.

13.9: DIFFERENT TYPES OF LARVAE & PUPAE

(A). Larvae:

There are three main types of insect larvae namely oligopod, polypod and apodous.

1) Oligopod: Thoracic legs are well-developed. Abdominal legs are absent. There are subtypes

a) Campodeiform: They are so called from their resemblance to the dipluran genus *Campodea*. Body is elongate, depressed dorsoventrally and well-sclerotised. Head is prognathous. Thoracic legs are long. A pair of abdominal cerci or caudal processes is usually present. Larvae are generally predators and are very active. E.g.: grub of antlion or grub of ladybird beetle.

b) Scarabaeiform: Body is ‘C’ shaped, stout and subcylindrical. Head is well developed. Thoracic legsa re short. Caudal processes are absent. Larva is sluggish, burrowing into wood or soil. Eg: grub of rhinocerous beetle.

2) Polypod or Eruciform: The body consists of an elongate trunk with large sclerotised head capsule. Head bears a pair of powerful mandibles which tear up vegetation. Two groups of single lensed eyes found on either side of the head constitute the visual organs. The antenna is short. Three pairs of thoracic legs and upto five pairs of unjointed abdominal legs or prologs are present. Thoracic legs are segmented and they end in claws which are used for holding typically bears rows or circlet of short hooked spines or crochets which are useful in clinging to the exposed surface of vegetation and walking. Abdominal segments three to six and ten typically bear prologs. **E.g.**: caterpillar (larvae of moths and butterflies).

a) Hairy caterpillar: The body hairs may be dense, sparse or arranged in tufts. Hairs may cause irritation, when touched. **E.g.**: Red hairy caterpillar.

b) Slug caterpillar: The larva is thick, short, stout and fleshy. Larval head is small and retractile. Thoracic legs are minute. Abdominal legs are absent. Abdominal segmentation is indistinct. Larva has poisonous spines called scoli distributed all over the body. Such larva is also called platyform larva.

c) Semilooper: Either three or four pairs of prologs are present. Prologs are either wanting or rudimental in either third or third and fourth abdominal segments. Eg: Castor semilooper.

d) Looper: They are also called measuring worm or earth measurer or inch worm. In this type only two pairs of prologs are present in sixth and tenth abdominal segments. Eg: Daincha looper.

3) Apodous: They are larvae without appendages for locomotion. Based on the degree of development and sclerotization of head capsule, there are three subtypes.

a) Eucephalous: larva with well-developed head capsule with functional mandibles, maxillae stemmata and antennae. Mandibles act transversely. Eg: Wriggler (larva of mosquito) and grub of red palm weevil.

b) Hemicephalous: Head capsule is reduced and can be with drawn into thorax. Mandibles act vertically. **E.g.**: Larva of horse fly and robber fly.

c) Acephalous: Head capsule is absent. Mouth parts consists of a pair of protrusible curved mouth hooks and associated internal sclerites. They are also called vermiform larvae. **E.g.**: maggot (larva of housefly).

(B). Pupa: It is the resting and inactive stage in all holometabolous insects. During this stage, the insect is incapable of feeding and is quiescent. During this transitional stage, the larval characters are destroyed and new adult characters are created. There are three main types of pupae.

1) Obtect: Various appendages of the pupa viz., antennae, legs and wings pads are glued to the body by a secretion produced during the last larval moult. Exposed surface of the appendages is more heavily sclerotized than that adjacent to body. **E.g.**: moth pupa.

2) Exarate: Various appendages viz., antennae, legs and wing pads are not glued to the body. They are free. All oligopod larvae will turn into exarate pupae. The pupa is soft and pale. **E.g.**: pupa of rhinoceros beetle

3) Coarctate: The pupal case is barrel shaped, smooth with no apparent appendages. The last larval skin is changed into a case containing the exarate pupa. The hardened dark brown pupal case is called puparium. Eg: Fly pupa.

13.10: POLYEMBRYONY AND PARTHENOGENESIS IN INSECTS

(a). Polyembryony in Insects

Sometimes an egg, instead of giving rise to a single larva, produces two or more. This is called polyembryony. It occurs occasionally in Orthoptera and perhaps in other groups, but in some endoparasitic insects it is a regular phenomenon. This is true, for instance, in *Halictoxenos* (Strepsiptera), and in a number of Hymenoptera including several genera of Encyrtidae and Ichneumonidae which parasitize the eggs and larvae of Lepidoptera, and Aphelopus and Platygaster. The eggs of all these parasites are small and relatively free from yolk. Nutriment is derived from the host tissues in which the developing embryos are situated.

(B). Parthenogenesis in Insects

Sometimes eggs develop without being fertilized. This phenomenon is known as parthenogenesis. Occasional parthenogenesis, following from the failure of a female to find a mate, is probably widespread, but a number of insects use parthenogenesis as a normal means of reproduction. It has been recorded from all the insect orders except Odonata, Dermaptera, Neuroptera and Siphonaptera. The sex of the offspring developing from an unfertilized egg is dependent on the sex-determining mechanism of the insect and the behavior of the chromosomes at the meiotic division of the oocyte nucleus. In the majority of insects, the female is homogametic (XX) and the male heterogametic (XY or XO), but the Lepidoptera are exceptional with the females having the heterogametic constitution.

13.11: SUMMARY

The first mitotic division of the zygote nucleus marks the start of embryonic development, which ends with hatching. Insects display a range of embryonic developmental patterns, whic-h is not surprising given their diversity in shape, function, and life history. However, as more information is gathered, certain evolutionary themes are starting to stand out. The majority of species' eggs have a sizable amount of yolk. In exopterygote eggs, the yolk predominates to the point where the cytoplasm is only clearly visible when it forms a small island around the nucleus. In some parasitic Hymenoptera and viviparous Diptera (Cecidomyiidae), whose eggs are yolkless and get nourishment from their surroundings, this trend toward a reduction in the relative amount of yolk in the egg has some significant ramifications. In general, endopterygotes have smaller (measured in relation to the size of the laying insect) and faster-developing eggs than exopterygotes. An expanded embryonic area from which development can occur is made possible by the enlarged cytoplasm because it causes more and larger cells to grow at the yolk surface more quickly. The growth of endopterygotes is more streamlined and straightforward than that of exopterygotes. When taken to an extreme, as seen in the apocritan Hymenoptera and cyclorrhaph Diptera, "reduction or elimination of ancestral irrelevancies" leads to the production of a structurally simple larva that hatches shortly after egg laying. However, developmental specializations linked to a growing divergence between adolescent and adult habits may be placed on this short-circuiting process.

13.12: TERMINAL QUESTIONS AND ANSWERS

Question No.1 Discuss what phase of embryonic development is the most crucial?

Question No.2 What are the 4 stages of embryonic development?

Question No.3 Explain about insect egg structure with suitable diagram.

Question No.4 write about different type of larvae and pupae.

Question No.5 Write difference between Polyembryony and Parthenogenesis in Insects.

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