M.Sc. Final Year
Zoology, Paper IV

INSECT PHYSIOLOGY

मध्यप्रदेश भोज (मुक्त) विश्वविद्यालय – भोपाल

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SYLLABI-BOOK MAPPING TABLE

Insect Physiology

Syllabi	Mapping in Book
UNIT - I: 1. Integument - Structure, function and modifications of insect integument. Moulting and sclerotization. 2. Structure and modifications of alimentary canal in different types of insects. 3. Food, feeding and digestion in insects. 4. Structure and physiology of respiratory organs in terrestrial, aquatic and parasitic insects. 5. Structure and function of haemolymph. Circulatory organs and mode of circulation in insects. 6. Physiology of Excretion. Salt and water regulation in insects.	**Unit-1:** Insect: Integumentary, Digestive, Respiratory, Circulatory And Excretory System **(Pages 3-88)**
UNIT - II: 1. Neuro-endocrine secretion in insects and its function. 2. General Plan of Nervous System in insects. 3. Structure and functions of various Visual organs in insects. Physiology of Vision. 4. Sound producing organs and mechanism of sound production. Types of songs and their significance. 5. Physiology of various types of mechano-receptors and chemoreceptors. Structure of various types of muscles in insects and its physiology.	**Unit-II:** Neuroendocrine, Nervous, Sensory and Muscular Systems **(Pages 89-172)**
UNIT - III: 1. Bioluminescence - Light producing organs, mechanism and its significance. 2. Pheromones - types, chemical nature and function. 3. Nervous integration - learning and memory. 4. Diapause in insects. 5. Mimicry in insects. 6. Insect Behaviour - Social life, Symbiosis and Adaptations.	**Unit-III:** Bioluminescence, Pheromones, Nervous Integration, Diapause, Mimicry And Insect Behaviour **(Pages 173-228)**
UNIT - IV: 1. Male and female reproductive organs in insects and their modifications. 2. Physiology of reproduction. Mating, transfer of sperm, Vitellogenesis sperm storage. 3. Polyembryony and Parthenogenesis. 4. Fertilization and development upto formation of germinal layers. 5. Various types of larva and pupa, their significance. 6. Metamorphosis in insects - types, theories and importance	**Unit-IV:** Reproduction, Fertilization, Development and Metamorphosis **(Pages 229-326)**

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INTRODUCTION

NOTES

Insects are the most varied group of animals on the planet. Their general body plan allows for such incredible shape diversity. Insects are arthropods, which means their internal tissues are protected by an exterior skeleton. The exoskeleton not only protects internal tissue, but it also permits sensory systems to work. Insects' skeleton is made up of integument, and this component of the insect has been the subject of a lot of research. The exoskeleton of an insect is extremely tough yet flexible, allowing for movement and providing attachment places for muscles. The exoskeleton can be compared to a hollow cylinder, which is stronger than a solid cylinder in terms of strength per weight, but has a higher surface area for the same weight.

The study of how insects survive and reproduce is known as insect physiology. This is a long-standing subject of study that is still being pursued today. Insect physiology is typically studied using a systems approach. These are the same systems that all animals require. The digestive, excretory, circulatory, immune, muscular, neurological, and reproductive systems are the primary systems.

This book, *Insect Physiology*, contains four units and is written with the distance learning student in mind. It is presented in a user-friendly format using a clear, lucid language. Each unit contains an Introduction and a list of Objectives to prepare the student for what to expect in the text. At the end of each unit are a Summary and a list of Key Terms, to aid in recollection of concepts learnt. All units contain Self-Assessment Questions and Exercises, and strategically placed Check Your Progress questions so the student can keep track of what has been discussed.

UNIT 1 INSECT: INTEGUMENTARY, DIGESTIVE, RESPIRATORY, CIRCULATORY AND EXCRETORY SYSTEM

Structure

1.0 INTRODUCTION

The word integument is derived from the Latin word integumentum, which mean a covering, that includes skin and its appendages-hair, nails and glands.

Integument plays an important role for the success of the insects. Insects constitute about 75% of all animal species on Earth. About one-half of this group feed on plants whereas the other half feeds upon dead plant material or animals or both dead and living material. The integument provides the principal barrier between internal body structures and the environment. The integument of insects comprises of the membrane, epidermis and cuticle. It is often thought as the skin of an insect but, functionally it provides physical protection to internal organs. Due to its rigidity, it serves as a skeleton to which muscles are attached. It also reduces water loss to a very low level in most insects, which is of great significance in the evolution of this predominantly terrestrial class. In addition to these primary functions, the cuticular component of the integument performs a number of secondary functions, such as it act as a metabolic reserve which is used as cyclically to construct the next stage, or during periods of great metabolic activity or starvation. It also prevents entry of foreign bodies, both living and nonliving. The integument is responsible for the colour of insects, especially the cuticular component.

Digestion of food in insects involves the chemical transformation of large and complex molecules to smaller molecules and absorbed through the gut wall for insect nutrition. Digestion is carried basically by enzymes that are coevolved with the food of the insect and the physicochemical conditions, especially pH in the insect gut. The digestive system consists of the alimentary canal (gut) and salivary glands, and is responsible for all steps in food processing: digestion, absorption, and feces delivery and elimination. These steps occur along the gut. The anterior (foregut) and posterior (hindgut) parts of the gut have cells covered by a cuticle whereas, in the midgut, cells are separated from the food by a film like anatomical structure referred to as the peritrophic membrane. Salivary glands are associated with the foregut and may be important in food intake but usually not in digestion. Remarkable adaptations are found in taxa with very specialized diets, such as cicadas (plant sap), dung beetles (feces), and termites (wood), and in insects with short life spans, as exemplified by flies and moths. Digestion is carried out by insect digestive enzymes, apparently without participation of symbiotic microorganisms.

An insect's respiratory system is the system with which it introduces respiratory gases to its interior and performs gas exchange. Air enters the respiratory systems of insects through a series of external openings called spiracles. These external openings, which act as muscular valves in some insects, lead to the internal respiratory system, a densely networked array of tubes called tracheae. This network of transverse and longitudinal tracheae equalizes pressure throughout the system. It is responsible for delivering sufficient Oxygen (O2) to all cells of the body and for removing Carbon Dioxide (CO2) that is produced as a waste product of cellular respiration. The respiratory system of insects is separate from the circulatory system.

After digestion of food, the insect circulatory system plays central role in delivering nutrients and hormones to cells and removes waste. Most insects have the dorsal vessel with the circulating portion of the extracellular fluid known as the haemolymph (blood). Unlike vertebrates, the insect circulatory system is open that means the haemolymph flows freely around insect organs. Through process of excretion insect maintains its internal environment within physiologic limits by eliminating the excess of metabolites.

Insects, like all other arthropods, have an open circulatory system which differs in both structure and function from the closed circulatory system found in humans and other vertebrates. In a closed system, blood is always contained within vessels, i.e., arteries, veins, capillaries or the heart itself. In an open system, blood is usually called haemolymph spends much of its time flowing freely within body cavities where it makes direct contact with all internal tissues and organs. The circulatory system is responsible for movement of nutrients, salts, hormones, and metabolic wastes throughout the insect's body. In addition, it plays several critical roles in defense as it seals off wounds through a clotting reaction, it encapsulates and destroys internal parasites or other invaders, and in some species, it produces or sequesters distasteful compounds that provide a degree of protection against predators. The hydraulic (liquid) properties of blood are important as well. Hydrostatic pressure generated internally by muscle contraction is used to facilitate hatching, molting, expansion of body and wings after molting, physical movements. In some insects, the blood aids in thermoregulation, it can help cool the body by conducting excess heat away from active flight muscles or it can warm the body by collecting and circulating heat absorbed while basking in the sun.

Excretion is the process of elimination of metabolic wastes and unwanted chemicals from its system. Metabolism is the sum total of all the chemical reactions occurring in the cells and body. The process of excretion is quite different to defecation, which is the removal of undigested food wastes from the gut. However, the gut of many animals also has a role in excretion as some materials may be excreted into the gut and eliminated with the faeces. In insects most excretory products are excreted into the gut lumen and eliminated along with faecal matter. Excretion is also important in eliminating excess water and other unwanted chemicals that may be ingested and enter the body fluids, such as plant poisons and excess salts.

The main excretory organ of the insect is the Malpighian tubule. Insects contain anything from 2 to 150 or more Malpighian tubules depending on the genus. Malpighian tubules are tubular outgrowths of the gut. They typically develop as pouches emerging from the junction between the midgut and the hindgut, though there actual final position varies - they may be attached to the midgut, hindgut or the midgut-hindgut junction as is the case with our ant above. Each Malpighian tubule is a blind-ending tube whose lumen is continuous with the lumen of the gut. Each consists of a single layer of epithelial cells, forming the tubule wall, enclosed by an elastic membrane.

In this unit, you will study about the structure, function and modifications of insect integuments, moulting and sclerotization, structure and modifications of alimentary canal in different types of insects their food, feeding and digestion system, structure and physiology of respiratory organs in terrestrial, aquatic and parasitic insects, structure and function of haemolymph, circulatory organs and mode of circulation in insects and physiology of excretion and salt and water regulation in insects.

1.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand structure and functions of integuments of insects
- Discuss the main parts and role of foregut, midgut and hindgut
- Explain the feeding and digestion physiology of insects

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- Understand the structure and physiology of respiratory organs in insects
- Discuss the function of haemolymph
- Describe mode of circulation in insects
- Explain role of Malpighian tubules in excretion

1.2 INTEGUMENT

The outermost layer of insect's body is called as integument or body wall. The integument mainly provides the outer shape of an insect and form exoskeleton, to which the muscles are attached. It protects the insect from various harms, such as mechanical damage, radiation, desiccation and invasion of pathogenic microorganisms.

1.2.1 Structure, Function and Modifications of Insect Integument

The structure of insect integument is discussed below:

Structure of Insect Integument

The body wall consists of inner layer of cells called as the epidermis, and an outside covering known as the cuticle that lies on top of the epidermis. Epidermis rests on the basal lamina (Refer Figure 1.1).

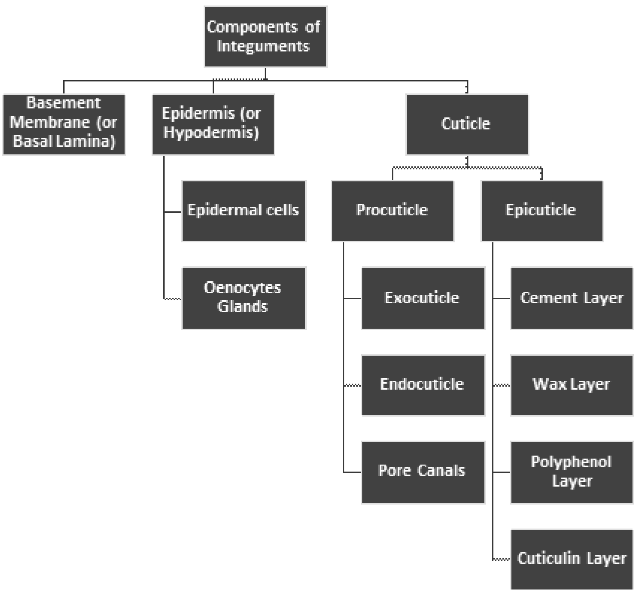

Fig. 1.1 *Components of Insect Integuments*

1. Basement Membrane

The epidermis lies on the basement membrane also called basal lamina. The basement membrane is the basal part of the body wall and seems like non-living shapeless granular layer. It has about 0.5μ thickness and composed of fibrous protein, glycosaminoglycans. The basement membrane produced from epidermal or other epithelial cells and reticular lamina synthesized by hemocytes and fat body cells. The basement membrane forms a continuous sheet below epidermis and where muscles are attached it is continuous with sarcolemma of the muscles.

2. Epidermis

Epidermis is an inner unicellular layer below endocuticle and lying on basement membrane. Epidermal cells are polygonal type which transforms in to cuboidal or columnar during moulting. These cells are composed of well-developed large nuclei and other cytoplasmic contents. Neighboring epidermal cells are held together through certain cytoplasmic processes**.** Epidermal cells are glandular and secrete cuticle and the enzymes involved in production and digestion of old cuticle during moulting. Thus, they have widespread Rough Endoplasmic Reticulum (RER) and Golgi complexes. Some cells of this layer are highly specialized and produce hairs and other surface structures.

Modifications: The epidermal cells get differentiated into various types of glands and cells based on the function they perform. These glands are as follows:

- Dermal Glands: It produces a cement layer.
- Trichogen Cells: They produce hair like seta or trichome.
- Moulting Glands: They secrete moulting fluid which digests the old cuticle.
- Peristigmatic Glands: They are found around the spiracles, for example in Dipteran larvae.
- Oenocytes: Oenocytes are named so because of their pale amber colour. These are considered as derivative of epidermal cells. Generally, they are large and polyploid cells with widespread tubular endoplasmic reticulum. Oenocytes are perhaps involved in lipid metabolism. They produce hydrocarbons including sex pheromones and other lipids that contribute to epicuticle.

3. Cuticle

Cuticle is outermost thick layer of integument and is mainly produced from the cells of epidermis. The cuticle has two layers namely; i. procuticle; and ii. epicuticle.

i. Procuticle: A thick inner layer of cuticle is called the procuticle. It is made up of mainly chitin, proteins and other compounds. Chitin is a chief component of procuticle and thus contributes to excellent mechanical properties of cuticle. On sclerotization, procuticle is differentiated into two layers namely exocuticle and endocuticle. Pore canals run across these two layers, i.e., as follows:

- **Exocuticle:** It is outer layer, darkly pigmented, hard and sclerotized. It provides rigidity to cuticle and made up of chiefly chitin and a hard protein termed sclerotin. Exocuticle is absent at regions where flexibility is needed, for example at joints.
- **Endocuticle:** It is inner layer, soft, light coloured and unsclerotized. It made up of more chitin but lacks hard protein sclerotin.

Pore Canals: These are thin vertical channels run across both exocuticle and endocuticle. It measures < 1m (0.1 – 0.15m) in diameter. They run perpendicularly from epicuticle throughout length of cuticle. They help in transportation of cuticular material and enzymes to outer procuticle and epicuticle.

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ii. **Epicuticle:** It is a thin outermost layer of cuticle and varies in thickness from 1-4μ. It provides the property of impermeability to entire cuticle. But it lacks chitin. Epicuticle has following four layers:

- **Cement Layer:** It is produced from dermal glands and is made of lipoprotein. It protects the insect body from external harm. It gives the size and shape to insect body.
- **Wax Layer:** It is prominent layer and measures about 0.25μ approx. in thickness. It is made up of long chain of hydrocarbons, esters of fatty acids and alcohols. Wax layer prevents water loss from the body.
- **Polyphenol Layer:** It is a non-static layer having different kinds of phenols which are mainly used in the formation of the proteins. Polyphenol layer is resistant to acids and organic solvents thus provide protection from external chemicals.
- **Cuticulin Layer:** It is an amber colour thin layer above epidermis and supported by outer polyphenol layer.

Composition of Cuticle: Basically, insect cuticle has two major compositions namely: i. chitin; and ii. proteins.

i. **Chitin**: Chitin is a nitrogenous polysaccharide having molecular formula of $(C_8H_{13}O_6N)_x$. Chitin constitutes 25-60% of dry weight of the cuticle. It is made up of high molecular weight polymer of anhydro-N-acetyl glucosamine residues linked by β-glycosidic linkages (Refer Figure 1.2). It is embedded with proteins in the procuticle to form glycoproteins. It is not soluble in water, alcohol, organic solvents, dilute acids and concentrated alkalies.

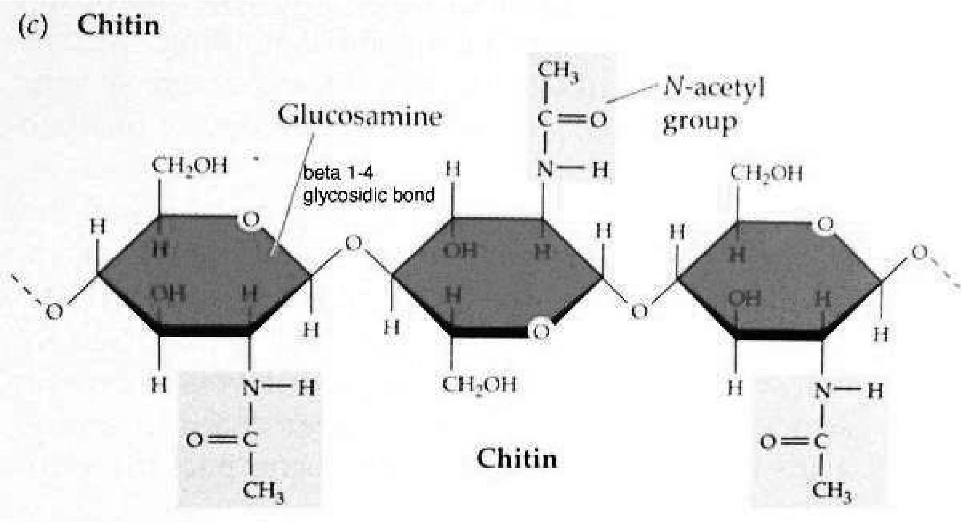

Fig. 1.2 *Chemical Structures of Chitin Which are Polymers of N-acetylglucosamine*

ii. **Proteins**: Cuticle has three types of proteins, they are as follows:

- **Arthropodin:** It is soft, untanned and water soluble protein found in endocuticle. The process of converting of arthropodin into sclerotin is referred as sclerotization or tanning.
- **Sclerotin:** It is amber coloured tanned cuticular protein and found only in exocuticle. This protein is insoluble in water.

- **Resilin:** It is a colourless elastic cuticular protein provides flexibility to sclerites, for example, wing articulatory sclerites.

Modifications of Cuticle

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Modifications of cuticle are as follows:

- Exocuticle of cockroach has only about 22% of chitin, while soft endocuticle has about 60%.
- In adult beetle, cuticle has a much more complex structure. Exocuticle is a simple alveolar tissue having no stratification or striation. But, endocuticle has horizontal bars, or trabeculae, arranged in well-defined strata. Trabeculae lie parallel in each stratum, but those of successive strata are crossed at certain angles.
- In grasshopper, melanin occurs in cuticle only in patches. Although exocuticle and endocuticle are colourless and transparent thus pigments are present in epidermis.
- Several pigments are found in cuticle (or in epidermis) that give an insect its typical colour. Also, in some beetles and flies, mineralized calcium as carbonate is accumulated so as to increase rigidity.

Outer Processes/Modifications of Integument: Outer processes of integument are divided in two categories namely cellular and non-cellular outgrowths. Out of cellular processes, some are unicellular and rests are multicellular (Refer Figure 1.3).

Non-Cellular Processes: These are non-cellular projections of outer surface of integument that are purely cuticular structures. They have the form of minute points or nodules, spicules, small spines and hairs.

Multicellular Processes: These are large, spine-like and hollow cuticular outgrowths of whole body wall and are thus lined by layer of epidermal cells. Immovable forms are spines and movable forms are called as spurs. For example, Locusts have spines on hind tibiae and spurs at ends of tibiae.

Unicellular Processes: Outgrowths of integument are hair like processes, known as setae that cover main body wall of most insects. Epidermal cell that forms a seta, or any hair like structure, is called as trichogen cell. With trichogen, there is a second cell that forms setal membrane. Setal membrane is floor of an alveolus or setal socket which has its generative cell called as socket-forming cell or tormogen (Refer Figure1.3).

Other forms are spine-like setae, plumose hairs, scales, cones, pegs, hooks, spatula, knobbed hairs, etc. For example, scales are powdery form when we touch body of moths and butterflies. When setae are innervated (supplied with nerve) form setal sense organs.

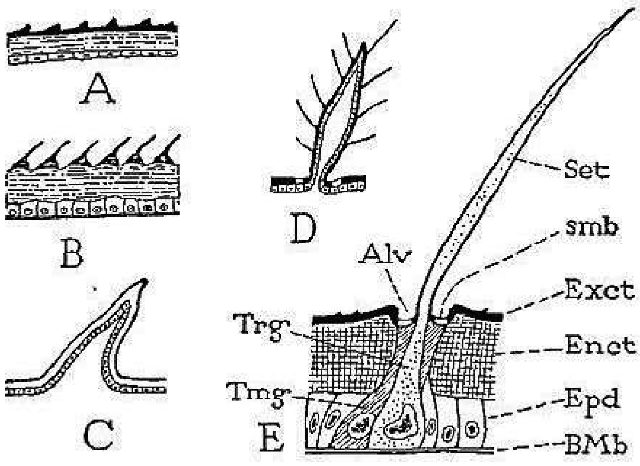

Fig.1.3 *Outgrowth Forms of Integument*

In above Figure 1.3, A and B show non-cellular cuticular processes, C and D show multicellular processes; and E show unicellular process or seta.

Note: Following are the abbreviations used in the above figure: Alv- alveolus, Set- seta, smb- setal membrane, Tmg- tormogen, Trg- trichogen.

Functions of Integument: Following are the important functions of integument and/or cuticle (exoskeleton) that are responsible for great success of insect species:

- **Body Structure:** It provides the structure, size and shape of the insect body. Cuticle gives support, stiffness and protection.
- **Water Loss:** Wax layer of cuticle gives water resistant property to integument. Thus, it prevents water loss due to evaporation in relatively dry environments. Also it helps to maintain an ionic balance in insect body.
- **Protection:** It serves as interface between insect and environment. It helps to prevent the entry of harmful chemicals. It protects the insect organs against physical harm and unfriendly organisms.
- **Pathogen Invasion:** It forms a barrier against invasion by pathogenic microorganisms and parasites. The epicuticle not only prevents adhesion needed for bacterial and fungal proliferation, it also has antibacterial and antifungal lipids and peptides.
- **Sensory Structures:** Parts of the cuticle are modified to form sense organs. The reception of external stimuli through these sense organs, such as specialized sensory hairs, processes or areas. These are involved in communication, either by providing pheromones or producing signaling structures and colours.
- **Locomotion:** It has important role in the locomotor system as muscles of the legs, wings, and movable sclerites are attached to cuticle (exoskeleton). The presence of hard, jointed appendages gives accurate movements possible with a minimum of muscle. It helps lifting the body off the ground and facilitates rapid movement. The stiffness and lightness of cuticle in formation of wings has made flight possible.
- **Abrasion of Gut:** Cuticular lining of foregut and hindgut protects their epidermis from abrasions that can occur by food passage.

- **Body Colour:** Colour of an insect depends on integument. Integument has various pigment molecules called chomophores which gives characteristic colours to different insects. For example, brown or black colour of many insects, such as beetles and cockroach are due to melanin pigment. Also pigments in cuticle give protective colouration against predators (through mimicry).

Integumentary System in Different Insects

Integumentary System of American Cockroach *(Periplaneta Americana)*, European honey bee (*Apis mellifera)* is discussed below:

I. American Cockroach *(Periplaneta Americana)*

The integument of cockroach is made up of three distinct layers namely; i. cuticle, ii. hypodermis; and iii. basement membrane (Refer Figure 1.4).

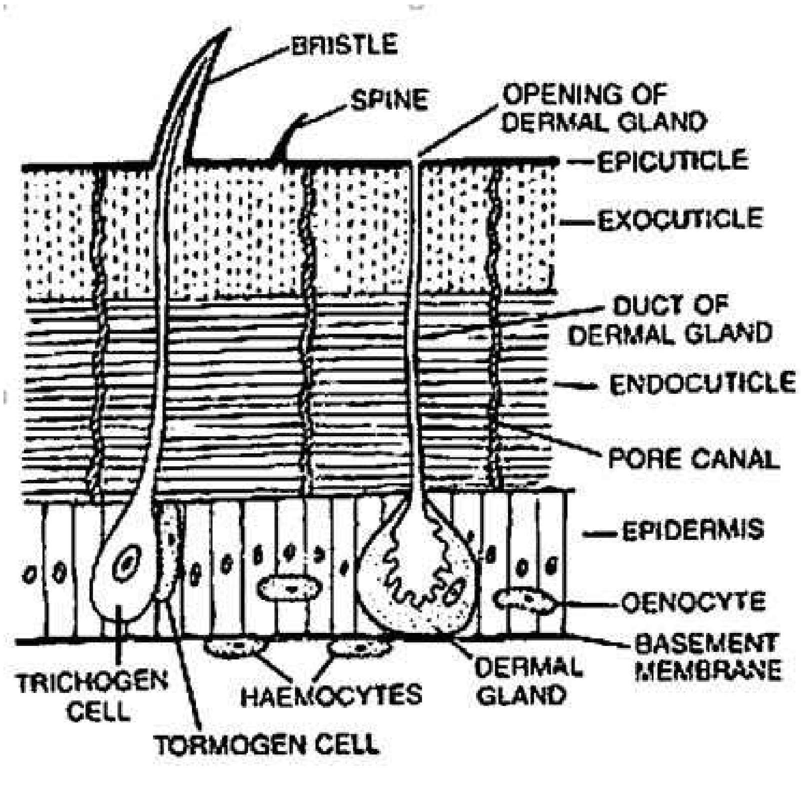

Fig. 1.4 *Transverse Section of Integument in Cockroach*

(i) Cuticle

Cuticle is a thick hard and brown coloured. It covers externally whole body of cockroach including appendages. Thus, the cuticle forms the exoskeleton in other insect. Hardened plates of cuticle are called sclerites, joints are called as sutures. Sclerites are joined through soft and flexible arthrodial membranes that enable movements of body and appendages. Head armour has many plates. Each of thoracic and abdominal segments has four sclerites namely a dorsal tergum, a ventral sternum and two very small lateral pleura.

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Cuticle also covers the foregut, hindgut, tracheal tubes and genital ducts. A number of invaginations of cuticle produce endoskeletons of head (called tentorium), thorax and abdomen (called apodemes). Also, the outgrowth of cuticle forms stiff immovable spines or bristles over the body and its appendages. Histologically, cuticle has exocuticle, endocuticle (both collectively called procuticle) and epicuticle.

- Epicuticle: It is outermost, very thin layer measures 1-2μ in thickness and lacks chitin. Outer part of epicuticle made of lipid or wax and inner part made of proteins and lipids.
- Exocuticle: It is middle layer measures 10-20μ in thickness. It is made up of chitin and has melanin pigments.
- Endocuticle: It is the innermost, thickest and laminated layer. It measures 20-30μ in thickness and made up of chitin.
- Pore Canals: These are hollow, spirally coiled tubes extending from epidermis up to endocuticle and exocuticle but not into epicuticle. About 12,00,000 pore canals are present per cm^2. These are perhaps filled with salt solution in ionic equilibrium with the hypodermis cells.

(ii) Epidermis

Epidermis is situated below cuticle that it secretes. It is highly organized and has columnar cells arranged in single layer. It rests on basement membrane and anchored into by hemidesmosomes. Epidermis resorbs endocuticle before each moult.

- Glands: Two types of dermal glands present in epidermis. These are associated with the secretion of cement layer and various types of cuticle. These glands may also secrete pheromones and certain hormones.
- Oenocytes: Adult cockroach has large irregular cells that measure >100μ in diameter. These cells seem between epidermal cells and basal lamina. These cells perhaps secrete wax or lipids that move to cuticle surface.
- Trichogen Cells: These are movable and hair like sensory setae, extending above cuticle surface. These are secreted from special cells of epidermis.

(iii) Basement Membrane

It is a dense and continuous sheet that attaches the inner surface of epidermis. It contains amorphous granular material perhaps mucopolysaccharides.

II. European Honey Bee (*Apis mellifera)*

The integument of honey bee is as follows:

- The cuticle has many layers lying above living cellular layer called Epidermis.
- Epidermis is attached to basement membrane which forms boundary between inside and outside of body.
- The layers forming cuticle are procuticle and epicuticle. In adult honey bee, procuticle is divided into endocuticle and exocuticle.
- Endocuticle basically contains chitin and this layer is relatively flexible. The exocuticle also contains chitin but also has sclerotin in large amounts. The sclerotin is very hard and dark in colour.
- The epicuticle is made of layers of sclerotin but has no chitin, the outer layer is waxy thus is a waterproof layer.

- The plates that make up exoskeleton of honey bee are termed sclerites and are formed through joining of exocuticle and epicuticle. Flexible membranous connections between plates are endocuticle.
- Some plates have inward growths (apodemes) of sclerites, these are places where the muscles attach or form strengthening to body. Outer surface of sclerites reflect the internal parts, forming grooves where internal structures are ridge, pits and pegs.
- In the honey bees, larvae and pupae have the flexible and colourless exoskeletons and adult has the rigid (highly sclerotized) and pigmented exoskeleton. Protein gives stiffness and elasticity to cuticle. In general, the soft cuticle has a much content of chitin (50% dry weight) than the stiff cuticles (15-30% dry weight). Integument of bees has about 50% protein, 22% chitin and 22% melanin.

Figure 1.5 illustrates integument of honey bee.

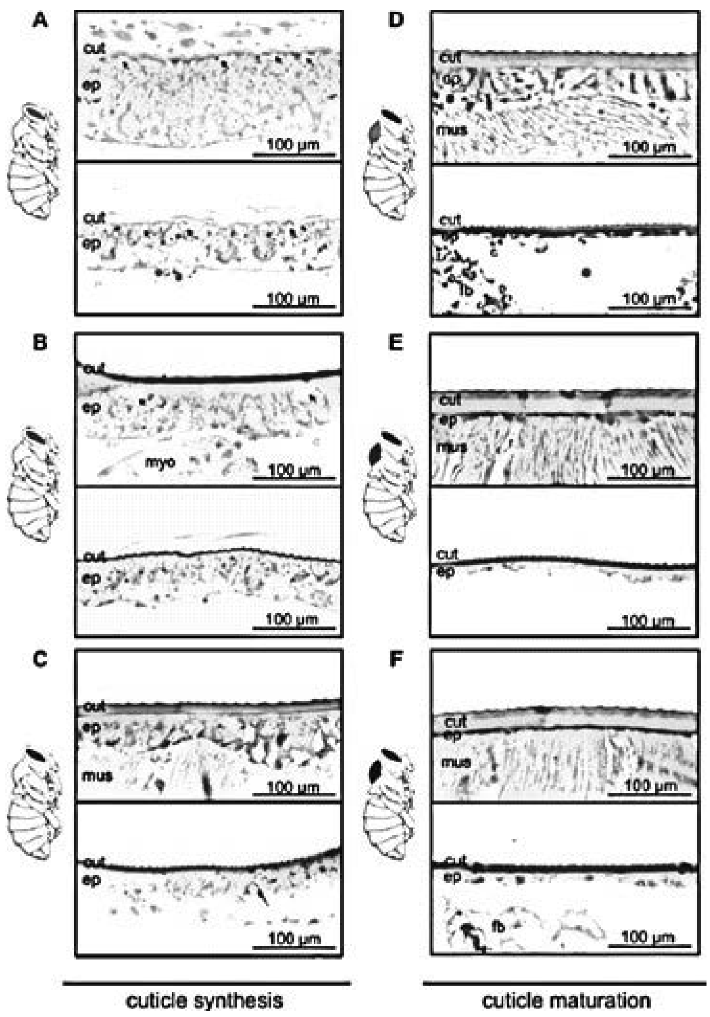

Fig. 1.5 *Integument of Honey bee*

1.2.2 Moulting and Sclerotization

The insect cuticle is hard non-elastic exoskeleton. Therefore, it needs to shed from time to time so as to allow the insects increase their size during growth period.

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Before the old cuticle is removed new cuticle has to be made below it, this process is called as **moulting**.

The cuticular parts removed during moulting are called as **exuvia**. Moulting takes place many times in an insect during the immature stages before becoming adult. The time interval between the two succeeding moulting is known as stadium and the stage formed by the insect in a stadium is known as **instar** (Refer Figure 1.6).

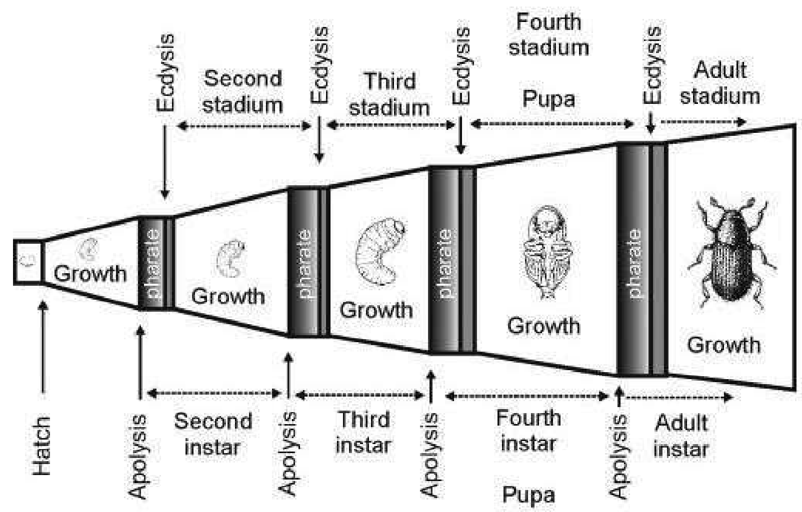

Fig. 1.6 *Different Stages of Insect Undergoing Moulting*

Summary of moulting process is given in Figure 1.7 below. Moulting in insect is a complex process that involves basically four phases, i. Apolysis, ii. Ecdysis, iii. Expansion; and iv. Sclerotization. Moulting initiates when epidermal cells divide to increase in number, become closely packed and columnar in shape (Refer Figure 1.8).

Step 1

Apolysis -- separation of old exoskeleton from epidermis

Step 2

Secretion of inactive molting fluid by epidermis

Step 3

Production of cuticulin layer for new exoskeleton

Step 4

Activation of molting fluid

Step 5

Digestion and absorption of old endocuticle

Step 6

Epidermis secretes new procuticle

Step 7

Ecdysis -- shedding the old exo- and epicuticle

Step 8

Expansion of new integument

Step 9

Tanning -- sclerotization of new exocuticle

Fig. 1.7 *Summary of Moulting Process*

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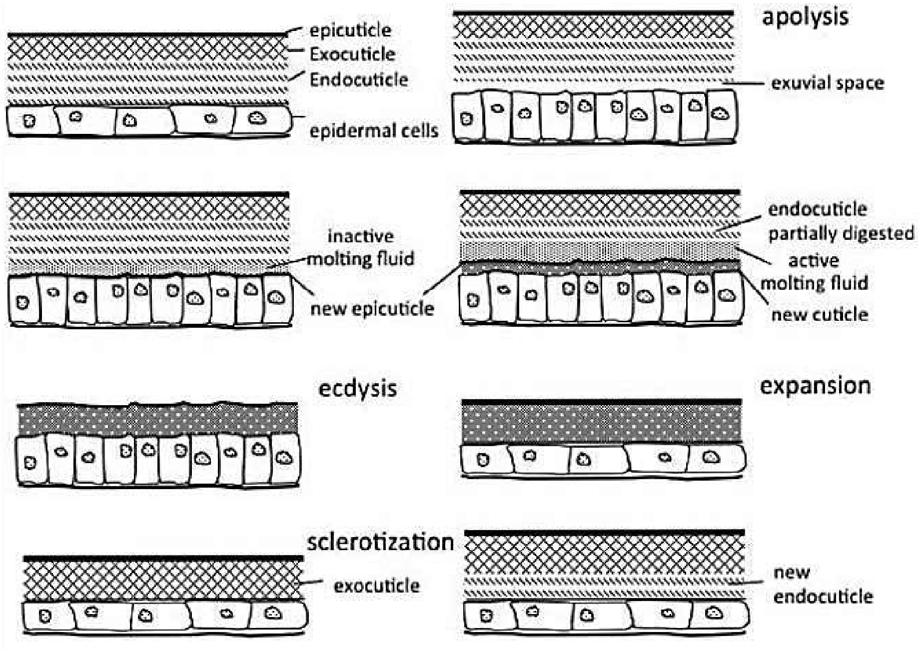


Fig. 1.8 *Schematic Representation of Moulting Process*

i. **Apolysis:** The dissolution of old cuticle and formation of new cuticle is known as apolysis. The old cuticle breaks away from the epidermal cells, leaving a sub-cuticular (exuvial) space below the old cuticle. This process caused by release of hormone ecdysteroids at the start of each moult. An inactive moulting fluid is secreted into sub-cuticular space. Initially moulting fluid is inactive so that it does not digest new epicuticle being made at this time. After formation of epicuticle the moulting fluid becomes active and begins to digest the old cuticle. After formation of new and undifferentiated cuticle (procuticle), insect undergoes ecdysis.

ii. **Ecdysis:** The process of the actual shedding of the old cuticle is called as ecdysis. The cuticle becomes very thin and weak along ecdysial lines by action of moulting fluid. The ecdysial lines are areas created in the cuticle that do not contain hardened exocuticle, as a result moulting fluid digests away most of cuticle along these lines.

    Many insects contain an inverted Y shape ecdysial lines along head and prothorax. These lines help in swallowing air or water so that an increased internal pressure is made and pump haemolymph into thorax to create more pressure on ecdysial lines. After breaking of old cuticle the insect pulls itself out. Initially head and thorax comes out of old cuticle. All cuticular parts are removed, together with the lining of foregut and hindgut and lining of most tracheae.

iii. **Expansion:** After ecdysis, there is continuous internal pressure to expand new epicuticle and undifferentiated new procuticle into new size and shape of subsequent instar.

iv. **Sclerotization**: The new cuticle is soft, milky and white coloured it sbecomes dark and hard by the process called as sclerotization. In this process, cross-links made between cuticle proteins so that they create rigid matrix in which chitin microfibrils can be embedded. Formation of cross-links between protein chains called as hardening or tanning. This tanning involves the differentiation of procuticle in to outer hard exocuticle and inner soft endocuticle. The sclerotization process also involves a typical colour change to tan, brown or black. This colour change occurs due to quinones that are tanning agents produced through melanization pathway.

Sclerotized Areas of Cuticle: Important feature of insect body wall is its ability to produce particular sclerotic areas in cuticle. Cuticles are soft and flexible, but at certain areas it becomes sclerotized, or hardened to form body-wall plates called as **sclerites**. The sclerites usually have definite shapes and interrelations with muscles constitute insect exoskeleton and have an important role in motor mechanisms for movements and locomotion of insect. There are some parts of body wall that are different from each other in sclerotization but have important role in movement, protection and growth of insect. These are sutures, apodemes and articulations.

Suture: Any kind of line or narrow space separating sclerotic areas of cuticle is called a suture. Sutures are flexible lines of integument between sclerites.

Apodemes: Any rigid ingrowths of integument are called apodemes. Cuticular part of an apodeme is usually enclosed in a layer of epidermis (Refer Figure 1.9 A, B, C) and but in some cases it is a solid cuticular ingrowth (Refer Figure 1.9 D). Area of a hollow apodeme is marked externally by a depressed line (suture) or a pit, depending on a type of apodemal invagination. During ecdysis cuticular part is withdrawn and regenerated. Apodemes usually take form of ridges, plates, or arms formed in multicellular invaginations of epidermis and they have definite mechanical purposes. It also provides site for attachment of muscles during moulting.

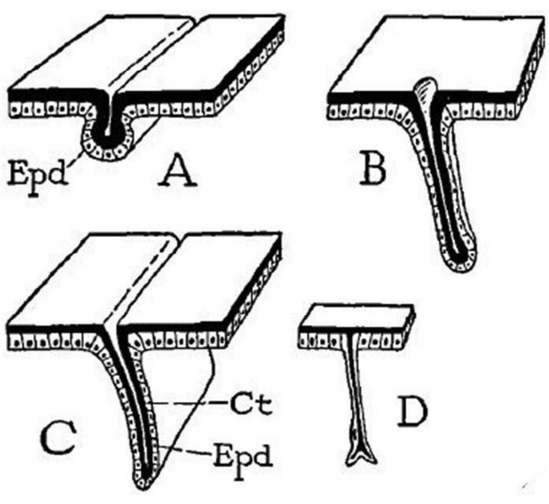


Fig.1.9 *Apodemes; A to C - Various forms of Multicellular Apodemes; D -Unicellular Apodeme*

Articulations: Wherever there is a line of movement in body wall that flexible area or joint is simply non-sclerotized cuticle between two neighboring parts of sclerotization. This movable area is called as an articular membrane or corium.

Check Your Progress

1. What is insect cuticle?
2. Define exocuticle?
3. Define the term moulting.
4. What are the steps of moulting?
5. Where are oenocytes present in the integument?

1.3 ALIMENTARY CANAL

In insects, digestive system or alimentary canal is a tube of epithelium running from mouth to anus. The main role of alimentary canal is to process ingested food by mechanical and chemical means so insect can absorb nutrients for their growth and development. Details of alimentary canal structures are explained below:

1.3.1 Structure and Modifications

The alimentary canal of insects has three main parts: i. foregut (or stomodeum), ii. midgut (or mesenteron); and iii. hindgut (or proctodeum) (Refer Figure 1.10). The alimentary canal is also commonly called as gut. All parts of insect gut are made of single layer of epithelial cells, bounded by basement membrane and striated muscle. The foregut and hindgut are ectodermal in origin, whereas midgut has endodermal origin. Cells of foregut and hindgut secrete cuticle. The cuticle lining of foregut and hindgut is known as **intima**. At each molt, intima is also shed and renewed.

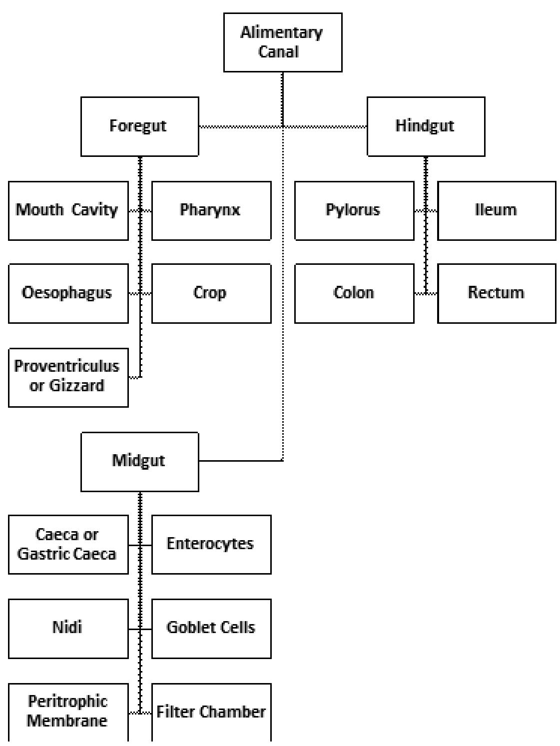


Fig. 1.10 *Parts of Alimentary Canal in Insects*

I. Foregut

Foregut (or stomodeum) is the anterior part of alimentary canal. In foregut, the food can be stored, filtered, and partly digested. The cells of foregut are flattened and undifferentiated as they are not usually involved in absorption or secretion.

The wall of foregut has three layers, as follows:

- Tunica Intima: It is secreted by the ectodermal cells.
- Epithelial Layer: It have glands with digestive function.
- Muscle Layer: It is composed of longitudinal and circular muscles.

Foregut is basically divided into five regions namely: i. buccal or mouth cavity, ii. pharynx, iii. esophagus, iv. Crop; and v. proventriculus.

i. **Mouth Cavity:** Mouth or buccal cavity is the initial part within the mouth. It opens into a narrow pharynx and is often indistinguishable from pharynx. It is the oral part of foregut.

ii. **Pharynx:** Exactly the actual initial part of the foregut is pharynx that links anteriorly with mouth cavity. Pharynx is situated within head and for most part below and in front of the brain. Pharynx is associated with ingestion and passing food back from mouth to esophagus. It has a well-developed musculature. The pharynx has a set of muscles known as dilator muscles.

Modifications: Dilator muscles are well-developed to form pharyngeal pump in sucking insects as they use it to suck fluids.

iii. **Esophagus:** The esophagus or oesophagus is a simple tube connecting the pharynx and crop. It serves to pass food back from the pharynx to the crop.

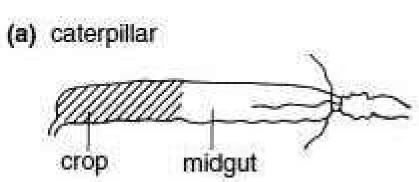
Modifications:

- It is poorly defined in hemimetabolous insects, but in many adult holometabolous insects it is a long, slender tube running between the flight muscles and back to the abdomen.
- The esophagus of some insects (for example caterpillars of *Myrascia bracteatella*) that feed on highly resinous plants has single or paired diverticula (Refer Figure 1.11d), in which the resin is stored.

iv. **Crop:** The crop is a storage organ is an extensible part of foregut just after the esophagus (Refer Figure 1.11a). During storage the food undergo some digestion in insects whose saliva contains enzymes or that regurgitate digestive fluid from midgut.

Modifications:

- In fluid feeder adults of Diptera and Lepidoptera, crop is a lateral diverticulum of esophagus (Refer Figure 1.11b,c).
- In some insects the intima of crop has spines or ridges which help in breaking up solid food into smaller particles and mixing in digestive fluid.



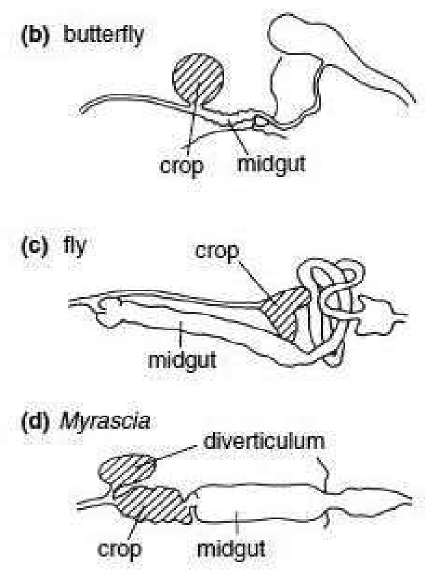


Fig.1.11 Storage Organ (Crop or Esophageal Diverticulum) in Foregut of Different Insects

Note: In above Figure 1.11 different parts in which food are temporarily stored are presented by hatching is shown.

v. Proventriculus or Gizzard

The proventriculus or gizzard is situated after the crop. The main feature of its structure is that cuticular lining or intima develops into prominent denticles. Proventriculus can act as a valve regulating rate at which food enters midgut, as a filter separating liquid and solid materials, or as a grinder to further break up solid material in food. The proventriculus is very variable in structure accordingly.

- When proventriculus work as a valve, its intima has longitudinal folds and circular muscle layer is thickened to form a sphincter. This valve or sphincter is called the esophageal or cardiac valve.
- When proventriculus act as a filter, it has spines that hold back solid material, allowing just liquid parts to move into midgut.
- When proventriculus works as gizzard and grinding up food, intima is formed into strong and radially arranged teeth, and a thick layer of circular muscle lines the whole structure.

Modifications of proventriculus in different insects are as follows:

- **Grasshoppers:** It forms a constriction at anterior of midgut and restrict movement of solid food from midgut to foregut, whereas allowing movement of liquids in both directions.
- **Ants:** These have a specialized proventriculus that separates partially digested food in the midgut from food in crop that has material used in trophallaxis.
- In **Cockroach**, **Locust** and **Cricket**, intima of proventriculus is developed into six strong cuticular plates or teeth that grind up the food.
- **Honey Bees:** Proventriculus is specialized to allowing them to retain nectar

in crop whereas pollen grains pass to midgut. The anteriorly directed part of proventriculus enables Honey bee to extract pollen grains from nectar in crop and posterior part of it extending into midgut, forms a valve.

NOTES

II. Midgut

The midgut (also called ventriculus/mesenteron/stomach) is the middle section of alimentary canal. It is of endodermal origin and, thus has no cuticular lining. The cells of midgut serve to secrete digestive enzymes or juices and to absorb the nutrients from digestion of food. Thus, the most part of digestion takes place in midgut. The midgut begins just at posterior foldings of stomodaeal valve of the foregut. The midgut ends just anterior to Malpighian tubules.

The epithelium is internally lined by a thin and transparent peritrophic membrane or envelop. The midgut is a simple tube and undifferentiated but some modified cells or structures are also present in midgut. These cells and structures vary with different insects, which are discussed below:

Enterocytes: Major cells of internal lining of midgut are tall and columnar cells and the membrane extended into numerous small, villi like folds called **microvilli**. The microvilli increase area of the cell membrane through which maximum absorption can occur. These cells are known as enterocytes or sometimes principal cells (Refer Figure 1.12). These cells secrete digestive enzymes and absorb nutrients.

Caeca: Many insects have finger like outgrowths at anterior end of midgut called caeca (or gastric or hepatic or enteric caeca). Crickets have two ceca; grasshoppers have six; cockroaches have eight; and some beetles and true bugs bear numerous ceca that vary in position. It increases functional area of midgut and houses symbiotic bacteria in some insects.

Nidi: Enteroendocrine cells in midgut epithelium are enteroendocrine cells secrete hormones that regulate function of the midgut and intestinal stem cells (Refer Figure 1.12), from which differentiated cells are produced. When the intestinal stem cells are present in groups, these are called as nidi.

Goblet Cells: In some insects there are also goblet cells in addition to principal cells. The midgut of Lepidoptera larvae has goblet cells, with a large flask-shaped central cavity. They play a role in regulation of the potassium level within haemolymph.

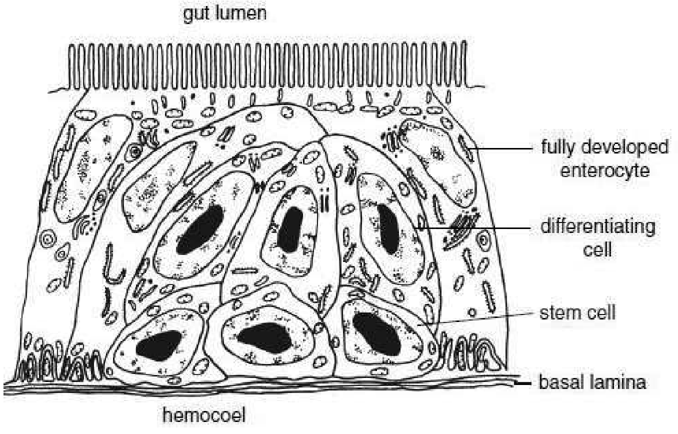


Fig. 1.12 *Group of Stem Cells (Nidus) and Enterocytes*

Peritrophic Membrane

The epithelium of midgut in most insects is internally lined by a thin and transparent membrane called as peritrophic membrane (or peritrophic envelop or peritrophic matrix). It is made up of proteins bound to a meshwork of chitin fibrils. It is lacking in many fluid feeding insects and in some Coleoptera. The functions of Peritrophic Membrane (PM) is as follows:

- It prevent mechanical damage to midgut epithelium.
- It prevent entry of microorganisms into body cavity.
- Binds potential toxins and other damaging chemicals.
- Divide midgut into an endoperitrophic space (between peritrophic envelope and midgut cells) and an ectoperitrophic space (in midgut lumen). This separation of epithelium increases digestion efficacy.

Types of Peritrophic Membrane

The peritrophic membrane can be categorized as follows:

- **Type I:** Produced by full length of midgut and found in Coleoptera, Blattodea, Ephemeroptera, Hymenoptera, Odonata, Orthoptera, Phasmida, larval Lepidoptera and adult Diptera.
- **Type II:** Produced by specialized tissues called cardia in anterior midgut and is present in Dermaptera, Isoptera, some Lepidoptera and larval Diptera.

Filter Chamber: In fluid feeding insects, gut has some modified structures to handle large intake of fluids and to rapidly eliminate large amounts of excess water. The anterior end of midgut brought into close contact with posterior of midgut (or anterior hindgut) and region of contact enclosed within a sac known as filter chamber. This serves rapid movement of water by osmotic gradient from lumen of midgut to hindgut. Hence, little amount of water in food passes along entire length of midgut.

III. Hindgut

The beginning of the hindgut is usually marked by pyloric valve and insertion of the Malpighian tubules. Like foregut, the hindgut is also lined by cuticular intima, but the hindgut intima is very thin and very permeable than that of the foregut. The functions of hindgut are to absorb water, salt and other nutrients from faeces and urine. The hindgut has three regions: i. the pylorus, ii. Ileum; and iii. Rectum.

i. Pylorus

The pylorus has well-developed circular muscle layer act as pyloric sphincter or valve. This valve regulates movement of food material from midgut to hindgut. The Malpighian tubules also enter gut in this region. Thus, the pylorus is a region in which food residue from midgut and secretions from Malpighian tubules are mixed.

Malpighian tubules act as excretory organs by removing nitrogenous wastes from haemolymph. The uric acid, a semi-solid waste is collected inside each tubule and is finely emptied into hindgut for removal as a part of faeces.

ii. Ileum and Colon

Generally, the ileum (or intestinum) is a narrow tube between pylorus and rectum. It conducts undigested food to rectum for final processing. Sometimes posterior part of ileum is markedly different and is called as **colon**. Usually, single type of cell is present in the ileum. The cells have extensive folding of apical plasma membrane with abundant closely associated mitochondria.

Modifications:

The function and form of ileum vary in some insects.

- In certain insects, some absorption of ions and/or water can take place in this part.
- In some species production and excretion of nitrogenous wastes occur in the ileum.
- In many wood-eating insects such as termites and beetles, the ileum is expanded to form fermentation chamber (or paunch) to house bacteria or protozoa that digest wood particles. The digestion products released by these microbes are absorbed across wall of the ileum.

iii. Rectum

The rectum is most posterior part of hindgut and is an enlarged sac. It has thin epithelial wall except for some areas where rectum has 6-8 rectal pads that are thick-walled and radially arranged (Refer Figure 1.13). In rectal pads, the epithelial cells are columnar. The rectal pads are main regions for absorbing ions, water, and small organic molecules from hindgut. The cuticle in rectal pads is unsclerotized and very thin than at other regions of rectum. The epithelial cells in each rectal pad are separated from heamolymph by sheath cells and a basal cellular layer.

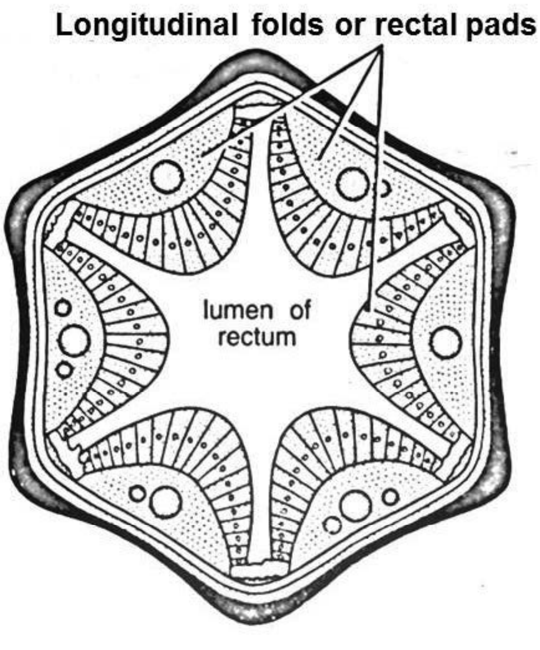


Fig. 1.13 *T.S. of Rectum in Cockroach*

1.3.2. Alimentary Canal in Different Types of Insects

I. Cockroach

In cockroach, alimentary canal is a long and coiled tube of uneven diameter. It has three regions as in other insects: i. foregut, ii. midgut; and iii. hindgut (Refer Figure 1.14).

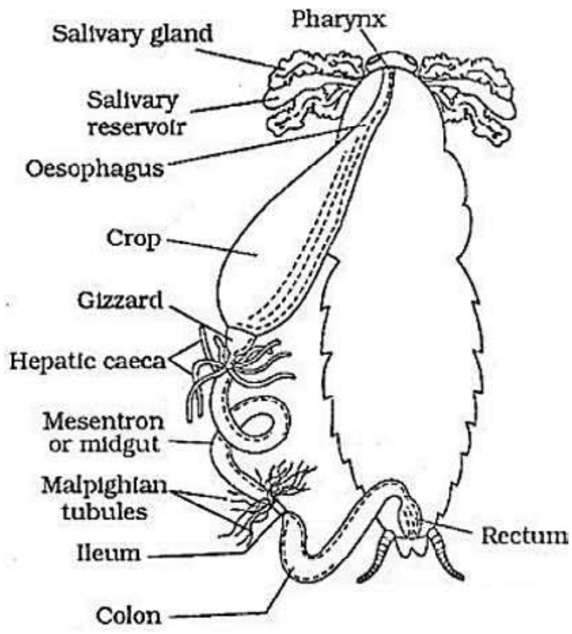


Fig. 1.14 *Alimentary Canal of Cockroach*

i. Foregut

It has mouth cavity, pharynx, esophagus, crop and gizzard.

- **Mouth Cavity:** It is also called as preoral chamber and is a small, undefined space outside mouth. Mouth cavity divided into two parts: a posterior part known as salivarium which has salivary duct opening and anterior part called cibarium that has narrow food passage towards mouth. Food is slightly processed by secretion or saliva from salivary gland in mouth cavity.
- **Mouth:** True mouth is a small opening at base of preoral cavity and connected to pharynx.
- **Pharynx:** It is a short tube structure and its intima (inside cuticular lining) is folded posteriorly.
- **Esophagus:** It begins after pharynx and is long straight narrow tube. It runs through nerve collar and enters thorax to connect with crop.
- **Crop:** It is a big, thin lined and pear shape chamber. It covers up to 3rd or 4th segment of abdomen. Crop is a bigger part of foregut. Internal epithelial lining and intima of crop are more folded. External surface of crop is covered by tracheal system. It serves as food storage organ.
- **Gizzard:** It is the last part of foregut and is a small cone shaped, thick walled and muscular sac. It has two parts: anterior armarium and posterior stomodaeal valve (Refer Figure 1.15).

- o **Armarium:** It has six internal longitudinal folds which reduce its lumen. Longitudinal folds are alternating with six longitudinal grooves that also have small secondary folds. Intima of each fold in anterior region has thick plate that creates centrally into strong, sharp teeth or denticles. Similarly in posterior part, intima of each fold has thin plate. After each longitudinal fold, the intima of gizzard has a soft pad called pulvillus having long backwardly directed hairs. These hairs work as strainers to allow smaller food materials to move into midgut.
- o **Stomodaeal Valve:** Posterior end of gizzard projects into midgut as a spout like narrow tube called stomodaeal valve. This valve folds back to form double lined structure. Function of this valve is to prevent back movement of food from midgut into gizzard.

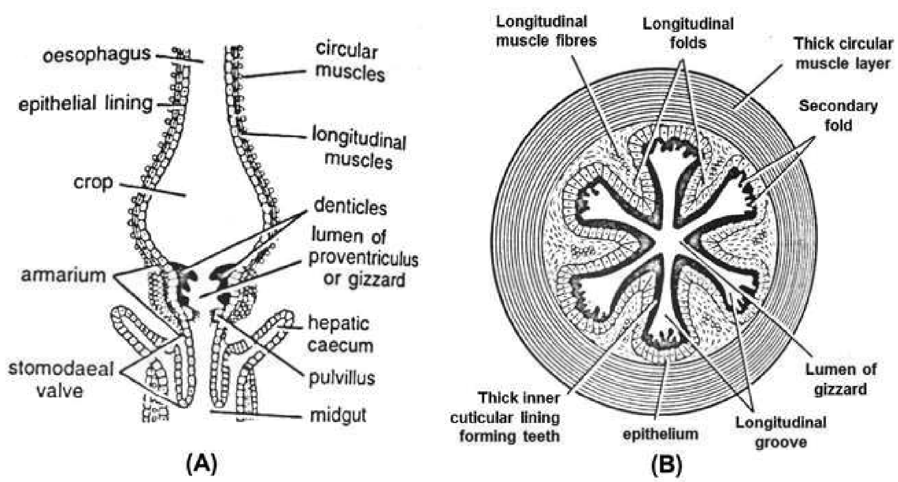


Fig. 1.15 *A. L.S. of Crop and Gizzard; and B. T.S. of Gizzard in Cockroach*

ii. Midgut

The middle part of alimentary canal is the midgut which is short and narrow tube. Inside wall of midgut is made up of glandular epithelium. Midgut works as true stomach and serves in digestion of food and absorption of nutrients.

- **Hepatic Caeca:** At anterior opening of the midgut, there are 7 or 8 short, narrow and hollow blind tubes known as hepatic caeca. Caeca are lined internally with epithelium and secrete digestive enzymes.
- **Malpighian Tubules:** At junction of midgut and hindgut, there are 80 to 90 threads like yellow colour tubules extending freely into haemocoel. These tubules are known as Malpighian tubules and act as an excretory organ. In cockroach these are known to have certain intracellular enzymes.

iii. Hindgut

Posterior part of alimentary canal is the hindgut. It has 3 regions: ileum, colon and rectum.

- **Ileum:** It is a short and thin tube and its posterior end has six minute triangular lobes. Internally these lobes have spicules which act as a sphincter.
- **Colon:** It is long and wide part and having an uneven form.

- **Rectum:** It an oval and spindle shaped chamber that has external ridges alternating with internal longitudinal thickening known as rectal pads (or rectal papillae or rectal glands). In cockroach, there are six rectal pads. Rectum opens to external of body through anus.

II. Honey Bee

Alimentary canal has role in food ingestion, its digestion, absorption of nutrients and excretion of waste products. In case of honey bee, it also acts as a carrier of nectar and honey. It has three parts: i. foregut, ii. midgut; and iii. hindgut. Followings are the features of each part (Refer Figure 1.16):

i. **Foregut:** It is an anterior part of alimentary canal. Foregut has **mouth, pharynx, esophagus, crop** (honey stomach or sac) and proventriculus.
   - Mouth leads into a suctorial pharynx, and then it continues as a narrow tube through thorax, petiole (constriction after thorax in bees) into abdomen. This is called **esophagus**.
   - Last dilated part of esophagus is known as **crop** or **honey stomach** (honey sac). In crop, excess nectar is collected, stored and transported to hive. In hive, it is regurgitated for conversion into honey.
   - The crop is followed by a neck like long and broad **proventriculus**. At its anterior end, it has four mobile lips, each armed with a number of spines. The four lips form an X shape aperture. The proventriculus has sceleritized teeth-like structure, and also muscles and valves (Refer Figure 1.16B). The function of proventriculus in the worker honey bee is to regulate the entrance of food from the crop to the ventriculus (midgut or real stomach). The nectar to be taken to the hive is retained in crop without being digested.
   - Proventriculus (stopper) works as a valve to separate foregut and midgut. This valve can grind and thrash food particles and filter pollen out of crop contents. Food passes through the proventricular valve and into the bee's midgut.

ii. **Midgut:** It is the functional stomach also called **chyle stomach** and is the largest part of intestine. In honey bees, it is a thick cylindrical tube bent upon itself in a U-shaped loop. It has role in secretion of enzymes, digestion and absorption of food materials. Malpighian tubules are small strands of tubes attached at end of midgut and functions to remove nitrogenous waste. The folds of its inner membrane increase the digestive surface. The peritrophic membrane protects epithelium from direct action of food and gives passage of digestive juices towards food and from these, when digested, towards absorption zone.

iii. **Hindgut:** The hindgut is last part of digestive system and divided into **ileum** (small intestine) and **rectum** (large intestine). The opening of hindgut is separated by a pylorus. The ileum is a short tube that connects midgut to rectum. The inner wall of coiled intestine is lined by longitudinal rows of chitinous teeth. The sac-like large intestine or rectum is posterior continuation of small intestine. Rectum has six rectal pads which help in salt and water regulation. The bees never eject waste materials in the hive. During prolonged cold winter, the waste material is retained in the expanded rectum.

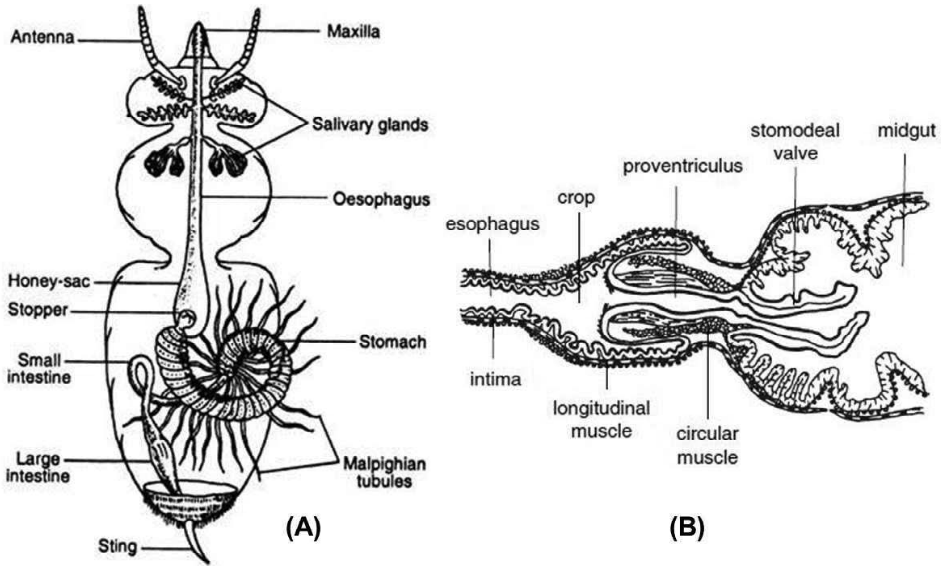


Fig. 1.16 *A. Alimentary Canal of Honey Bee; and B. Proventriculus in Worker Honey Bee*

(3) Housefly

Alimentary canal of housefly have three parts, i.e., i. foregut, ii. midgut; and iii. hindgut. Followings are the features of each part:

i. **Foregut:** Food is taken up by pharynx and passes via the esophagus either to crop, which is part of the foregut, or through proventriculus to the midgut (Refer Figure 1.17).

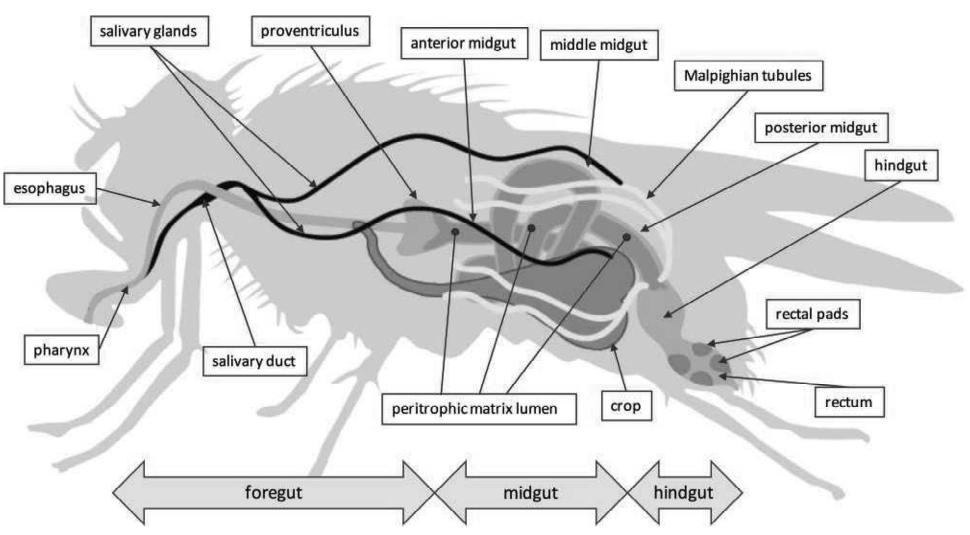


Fig. 1.17 *Alimentary Canal of the Adult Housefly*

ii. **Midgut:** Food materials that pass through proventriculus are enclosed in peritrophic membrane and cannot be regurgitated. The Peritrophic membrane is synthesized by cardia, a region of specialized cells that adjacent to proventriculus.

iii. **Hindgut:** There are teeth-like projections on lumen of hindgut. Water reabsorption occurs in the hindgut and rectum. Faeces entry into rectum is controlled by rectal valve. Rectal pads assist in removing waste from rectum as well as water absorption. In the foregut and hindgut, epithelial cells of fly alimentary canal are protected from ingested bacteria by a cuticular lining.

Check Your Progress

6. What is alimentary canal in insects?
7. Where is resin stored in insects?
8. In which part of alimentary canal, goblet cells are found?
9. What is role of peritrophic membrane in insect?
10. Define the term caeca. In which part of insect gut, it is found?

1.4 FOOD, FEEDING AND DIGESTION IN INSECTS

Food, feeding and digestion in insects is discussed below:

1.4.1 Food

There can be four broad categories of insects based on what they feed, they are as follows: i. plant feeders, ii. predators, iii. scavengers; and iv. parasites. Within each of these categories, they have different feeding mechanisms, such as biting and chewing on leaf or animals and sucking from plant or animal tissues.

- **Plant Feeders:** Phytophagous insects feed on plants and these insects mainly belong to orders, such as Orthoptera, Lepidoptera, Homoptera, Thysanoptera, Phasmida, Isoptera, Coleoptera, Hymenoptera and some Diptera. Phytophagous insects are also called herbivores.
- **Predators:** Insect predators eat basically other insects and are belong to orders Odonata, Mantodea, Heteroptera, Mecoptera, Diptera, Coleoptera, and Hymenoptera. Predator species have biting and sucking types of feeding. Predator insects are also known as carnivores.
- **Scavengers:** Saprophagous insects are scavengers as they feed on dead or decaying plant and animal tissues. These insects belong to many orders, such as Blattodea, Isoptera, Coleoptera, and Diptera. Saprophagous insects can be omnivores as they are feeding on both plant and animals.
- **Parasites:** A parasitic insect feed and complete its development in one host that may be other insect species or other animals. Host may or may not die until parasite completes its development. Insect parasites may also be called as parasitoids are host-specific wasps or flies from Hymenoptera and Diptera and most are tiny in size. Therefore, parasitic insects are carnivores.

Food of Cockroach: Cockroach is omnivorous, feeding any type of animal or plant matter. Generally, it feeds at night. They mainly like starches, sweets, greasy foods, and meats. For instance, they feed on wood, book-binding, cloth, leather, paper, pastes, glues and hair.

Food of Honey Bee: Worker honey bee collects pollen and nectar of various kinds of flowers and regurgitate into hive for feeding their castes and making honey.

Food of Housefly: Houseflies have an important ecological role in decomposing and recycling organic matter. Adults are mainly carnivorous; their main food is animal matter, carrion, and feaces. They also feed on milk, sugary material, rotting fruit and vegetables.

Nutritional Requirements of Insects

Generally, insects have similar nutritional requirements since their chemical compositions and metabolic capabilities are almost identical. But differences in insects occur since their adaptations to particular diets or they have different microorganisms which give particular nutrients.

Amino Acids: Amino acids are used for synthesis of proteins and enzymes for transport and storage, and as receptor molecules. Tyrosine is needed for cuticular sclerotization and tryptophan for production of visual pigments. ã-aminobutyric acid and glutamate are neurotransmitters.

Carbohydrates: Simple sugars, starch and other polysaccharides, are essential components of diet in insects. They are used as respiratory fuel.

Lipids: Fatty acids, phospholipids and sterols are components of cell membranes and have other specific functions.

Vitamins: The chief water-soluble vitamins required by insects are vitamin C (ascorbic acid) and the B vitamins. Among fat soluble vitamins, insects require vitamin A complex (β-carotene and related carotenoids) and vitamin E (tocopherols).

Minerals: Many metal ions for example, copper, iron, magnesium, etc. are required as coenzymes and in metalloenzymes.

1.4.2 Feeding

Based on food insect eat, different feeding mechanisms they have: biting and chewing on leaf or animals and sucking from plant or animal tissues. Generally, insect mouth parts are consists of paired append-ages like mandibles, maxillae and la-bium. The other parts that contribute in formation of mouth parts are hypopharynx and labrum.

Modifications in Mouthparts

Different insects have adapted themselves to different modes of ingestion of food. The basic structure of mouthparts remains the same. Holometabolous insects have different types of mouthparts in their larvae and adults. Hemimetabolous insects have similar type of mouthparts in their larvae or nymphs and adults.

The form of mouthparts varies widely in different insects. There are five types of mouthparts, given as follows:

- Biting and chewing, for example cockroach.

- Chewing and lapping, for example worker honey bee.
- Piercing and sucking, for example mosquitoes.
- Sponging, for example housefly.
- Siphoning, for example butterflies and moths.

i. Biting and Chewing Mouthparts: Cockroach

The mouthparts of cockroach are biting and chewing type. The other examples include grasshopper, dragonfly and beetle. The larvae of mosquito, housefly butterfly and honey bee also have biting and chewing mouthparts.

The mouthparts of cockroach are developed to suit its habit of feeding on solid food and as a result it has well developed mandibles. These mouthparts help the cockroach to bite and chew on hard stuffs, consume soft stuffs and also lap upon liquids. The mouthparts have labrum, mandibles, a pair of first maxillae, labium, and hypopharynx (Refer Figure 1.18). The following is the detail of these mouthparts:

- **Labrum:** The labrum is a broad lobe attached to clypeus in front of mouth. Labrum is also called as upper lip. On its inner side it is membranous and has some gustatory sensilla. Labrum helps in tasting and also handling the food.
- **Mandibles:** Mandibles are a pair of triangular, hard, unjointed, stout, chitinised structures. These are located on either side of mouth behind labrum. Mandibles are dentate along their inner margins and help in mastication of food. These mandibles have two pairs of muscles called as adductor and abductor muscles that help movement of mandibles only in horizontal plane against each other.
- **Maxillae:** The maxillae occupy a lateral position, one on each side of head behind mandibles. Maxilla has two basal segments. One of the segments is called cardo and is attached to head capsule. Another segment is a flat plate called the stipes attached to the cardo. Both cardo and stipes are loosely joined to the head by a membrane so that both are movable. On anterior of the stipes, there are two chitinous lobes called as an inner lacinia and an outer galea. Lacinia is like pincer having two terminal denticles while galea is outer soft hood like structure having long chitinous bristles. Each of stipes has five segmented maxillary palp on its outer side. This palp is located on a small sclerite known as palpifer. The maxillary palps help in cleaning the antennae and first pair of legs.
- **Labium**: The labium has similar structure as that of the maxillae. But labium has the appendages of two sides fused in the midline so that they form a median plate. In other words, labium is the fusion of second pair of maxillae. It is also called as lower lip. The basal part of labium is known as postmentum. Labium has two segments; one is broad rectangular submentum and another is triangular mentum. Prementum is also located in front of the mentum. Prementum is formed from fusion of maxillary stipes and it has a small sclerite known as palpiger. Each palpiger bear a three segmented labial palp. Anterior of prementum has a pair of paraglossae inner to labial palps. A pair of glossae is located between paraglossae.

- **Hypopharynx:** The hypopharynx is a median lobe immediately behind the mouth. It is chitinous, grooved and a rod-like structure and hanging into preoral cavity. It is also called as tongue. Hypopharynx splits the proximal part of preoral cavity into a larger anterior cibarium and a posterior salivarium. The salivary duct opens into salivarium at base of hypopharynx.

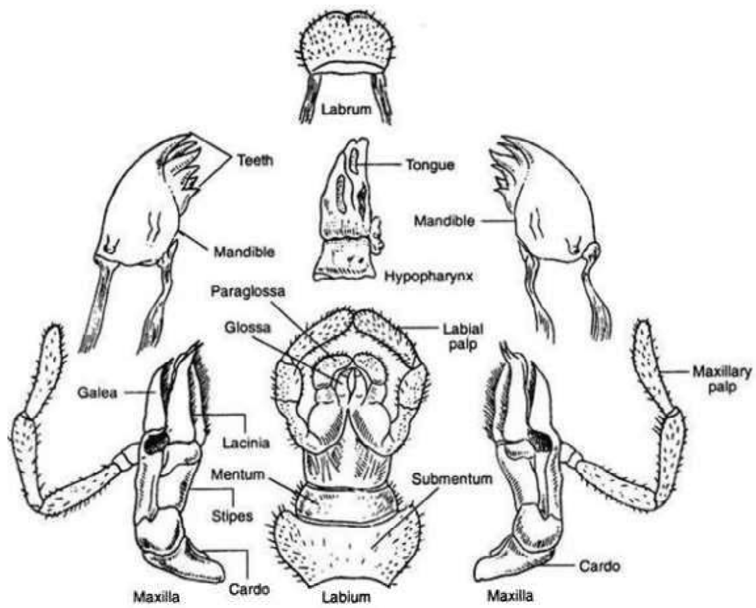


Fig. 1.18 *Biting Mouthparts of Cockroach*

Feeding Process in Biting and Chewing Insects: Cockroach

Biting and chewing insects make regular opening and closing movements of the mandibles. Both locusts and caterpillars generally make up to four bites per second when feeding constantly. But the rate varies with temperature, the type of food and feeding condition of insect. As a result of a sequence of bites, the insect cuts off a fragment of food. It is pushed back toward the mouth by mandibles and helped by the maxillae. Periods of continuous biting are separated by short gap for swallowing the food.

In cockroach, food is searched by sweeping antennae. It is tasted by maxillary and labial palps. The searched and tasted food is held by forelegs mouthparts, such as labrum and labium. During feeding, mandibles and maxillae have a sideways movement. This movement is induced by the action of the adductor and abductor muscles. Thus these movements bring mastication of food into fine parts.

ii. Chewing and Lapping Mouthparts: Honey bee

Honey bee has chewing and lapping mouthparts. Bumble bees also have similar mouthparts. As honey bees have both mandibles and a proboscis they can both chew and suck (Refer Figure 1.19A).

- **Mandibles:** The mandibles are a pair of jaws attached to head. Insect uses them to chew wood when restructuring the hive entrance, to chew pollen and to mould wax to build honeycomb. They also allow any action that needs a pair of grasping tools.

- **Proboscis:** It is a temporary functional organ in honey bee. It is made temporarily by collecting parts of maxillae and labium to create a tube for drawing up liquids, for example sweet juices, nectar, water and honey. After using proboscis honey bee withdraws and folds it back below head.
- **Labellum:** The glossae are very long so as to make a hairy, flexible tongue. The glossa is used for collecting honey and it is an organ of touch and taste. The glossa ends into a small circular spoon shaped lobe known as labellum. Labellum is used to lick the nectar.
- **Maxillolabial Parts:** Maxillolabial parts are modified to form lapping tongue. This tongue part is made of two galeae of maxillae, two labial palps and a long flexible hairy glossa of labium.

Feeding Process in Chewing and Lapping Insects: Honey Bee

The galeae fit tightly lengthwise, against elongated labial palps. Eventually, they cover the elongated glossae (tongue) to form a temporary food tube through which saliva is released. The tongue (glossae) is thrust into flower, so that it gets smeared with nectar. It is then retracted between labial palps and galeae. Nectar is then sucked by galeae and is dropped in chamber created by paraglossae. Collected nectar is then drawn into esophagus by pharyngeal pump.

iii. Piercing and Sucking Mouthparts: Mosquitoes

Sucking mouthparts are modified for piercing tissues of animals and plants to suck blood and plant juice. It is present in dipteran insects, for example mosquitoes and hemipteran insects like bugs, aphids, etc. This type of mouth arts is present in almost all the bloodsucking insects like tsetse fly, bed bug, etc. These mouthparts have long and pointed stylets. The number of stylets differs with different insects. Bugs have only maxillary stylets and mandibular stylets. In female mosquitoes, labrum-epipharynx and hypopharynx along with maxillary stylets and mandibular stylets are also found (Refer Figure 1.19B). The following is detailed structure of mosquito mouthparts:

- **Labium:** It is a long, fleshy and flexible tube with dorsal groove and also known as proboscis. The labium has two lobes at its end known as labella. Labella are like reduced labial palps. The other mouthparts such as mandibles, maxillae and hypopharynx are bounded in groove of labium.
- **Labrum-Epipharynx:** This is a compound structure made from fusion of labrum and epipharynx. Labrum-epipharynx is a stylet that has a ventral groove.
- **Hypopharynx:** It is a long flat needle like stylet. It forms food channel with labrum-epipharynx for sucking blood. It also has salivary duct that discharges saliva into blood of warm blooded animals.
- **Mandibles and Maxillae:** Two mandibles one on either side form stylets having blade like tips. They are used to create a wound in skin of host animal. Likewise first pair of maxillae forms stylets having serrated tips. Each maxilla has a maxillary palp.

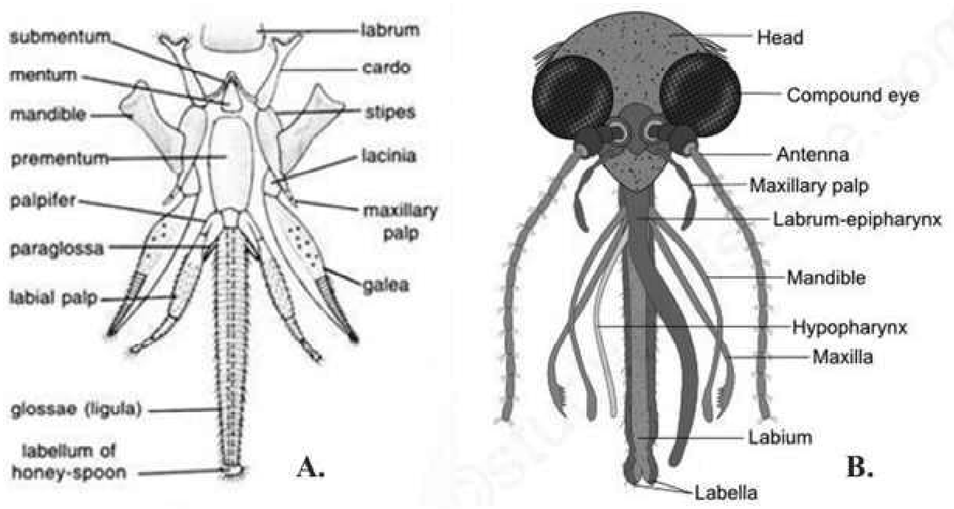


Fig. 1.19 *A. Chewing and Lapping Mouthparts of Honey Bee; and B. Piercing and Sucking Mouthparts of Female Mosquito*

Feeding Process in Piercing and Sucking Mouthparts: Mosquitoes

When a female mosquito sits on a host skin, it presses proboscis against skin. The flexible proboscis bends and mandibles together with maxillae create a wound on host skin. The labrum-epipharynx and hypopharynx are pierced into wound. The serrated tips of maxillae keep the wound open. The sucking action of muscles of cibarium and pharyngeal muscles help in sucking blood through the food channel. The saliva is injected into the blood by hypopharynx. This saliva of mosquito contains haemolysin that act as anti-coagulant of blood. This bite of mosquito causes itching and mild inflammation and thus mosquito feeds on blood.

iv. Sponging Mouthparts: Housefly

This type of mouthpart is modified for sucking up liquid or semi-liquid food. Housefly feeds on organic matter, open food or open wound and faeces. It sucks liquid part of the food material. Sugars containing solid foods are scrapped and liquefied by its saliva for sponging. The proboscis is long, fleshy and retractile, it extends downwards from head. The proboscis is dividable into rostrum, haustellum and labellum. Labium modified to haustellum and labellum (Refer Figure 1.20A). Mandibles are completely lacking in housefly mouthparts.

The following is the detailed structure of mouthparts:

- **Rostrum:** It is a basal part of the proboscis and is attached to the head capsule. At anterior, it is connected with the haustellum by a hinge joint. Pharynx and salivary duct are enclosed in rostrum. Pharynx connected with the food channel. First pair of maxillae is a pair of unjointed palps that are attached on rostrum.
- **Haustellum:** It is a middle part of the proboscis and has a median groove on its dorsal side. The hypopharynx with salivary canal and labrum-epipharynx are enclosed in the groove. They together form a food canal. Haustellum has a theca below it.

- **Labellum:** The terminal part of proboscis is enlarged, sponge like and two lobed that works as suction pads. The two lobes are known as labella. Labella have several grooves held by semi-circular chitinous rings. They seem like tracheae and therefore called as pseudotrachea. All pseudotrachea of both labella form capillary canals which collect liquid food and carry it to the canal. Labella act as sponging organs and are able to take exposed fluids. Labellum has sense organs of taste and smell. These insects also spit enzyme with saliva onto solid foods to liquefy them.

Feeding Process in Sponging Mouthparts: Housefly

When a housefly sits on the food, the haustellum and labella are thrust out and labella are pressed against food. Prestomial teeth under labella break small food particles and some solid is mixed in saliva that discharged on food. This liquefied food moves into pseudotrachea by capillary action up to mouth, via food channel.

Note: In the female horseflies which also possess sponging type of mouthparts, mandibles are present. The mandibles in these flies are useful in slicing skin and then blood which is exposed is sponged up.

v. Siphoning Mouthparts: Butterfly

This type of mouthparts is modified ideally for sucking flower nectar and fruit juice, present in adult butterflies and moths (order Lepidoptera). Immature stages, i.e., larvae of moths and butterflies have chewing mouthparts. Siphoning mouth parts include small labrum, coiled proboscis, reduced or absent mandibles and labium (Refer Figure 1.20B). The hypopharynx and epipharynx are absent.

- **Labium:** It is reduced to a triangular sclerite plate joined to front clypeus of head and has reduced labial palps.
- **Mandibles and Maxillary Palps:** Mandibles are absent or reduced (vary with the species). Maxillary palps are present in a reduced condition.
- **Proboscis:** It is formed from well-developed galea of first maxillae. It is very long semi tube like structure. The two galeae are locked with help of pegs and sockets to form proboscis. It is grooved internally to form the food channel or canal through which food is drawn up to mouth. When proboscis is not in use, it is tightly coiled beneath the head but it becomes extended in response to food stimulus.

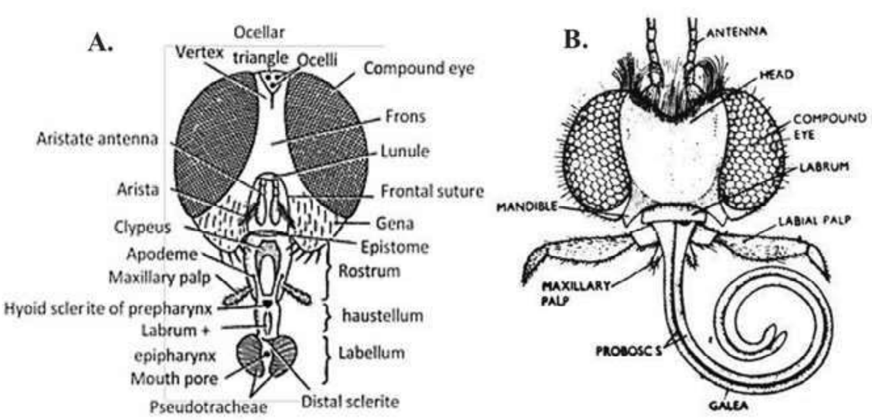


Fig. 1.20 *A. Sponging Mouthparts of Housefly; and B. Siphoning-Sucking Mouthparts of Butterfly*

Feeding Process in Siphoning Mouthparts: Butterfly

Insects with siphoning mouthparts do not chew their food. But they have a siphon-like structure which permits them to suck fluid into their body. This feeding is like to putting a straw into a drink to withdraw fluid. At the time of feeding, the proboscis which is coiled like a spring is uncoiled due to high pressure of haemolymph. This pressure is created in the stipes present on each galea. Coiling caused due to elasticity of cuticle of galea together with action of the intrinsic muscles. The uncoiled proboscis pushes out into the nectaries of flower. Because of the sucking action of cibarium muscles and pharyngeal muscles, the nectar is sucked up.

Digestive or Salivary Glands

Digestive system is the most conspicuous organ system in the body. It consists of the mouthparts, a long alimentary canal and a pair of salivary glands. Details of alimentary canal and mouthparts are already described. The following are the features of salivary glands:

Structure of Gland: The salivary glands of most insects are acinous glands. But in Lepidoptera, Diptera and Siphonaptera (fleas) they are tubular, with the ducts swelling to form the terminal glandular parts.

Functions of Saliva

Following are the functions of saliva:

- Saliva works to lubricate mouthparts. More is formed if food is drier.
- It has enzymes that start digestion of food. For example, an amylase that catalyze conversion of starch to sugar and an invertase for conversion of sucrose to glucose and fructose, are generally found.
- In blood sucking insects, no digestive enzymes present in saliva. But it has a group of components, known as sialome. Sialome helps feeding and overcome the hemostatic responses of host. The saliva of some blood sucking insects has an anti-coagulant.
- In many insects, saliva has some specific enzymes that help penetration and digestion of food. For instance, leaf-cutting ants have a salivary chitinase that attacks chitin in the fungus on which the insects feed and larval warble flies that bore into subcutaneous tissues of cattle, secrete a collagenase helps in movement of larva through host tissues.
- The mutual or unilateral exchange of alimentary fluid, including saliva, is called **trophallaxis**. Oral transfer of regurgitated liquid from one adult to another is a typical feature of social Hymenoptera, for example wasps, and *Formica fusca* ants.

Salivary Gland in Cockroach

Salivary gland in cockroach is situated in thorax on either of dorso lateral sides of esophagus. It is a pair of bipartite, diffuse and whitish in colour. Each gland has many secreting lobules or acini in grape like clusters joined together with thin tubules. Acini have two kinds of cells namely zymogenic cells and ductule containing cells. These cells secrete saliva that zymase and mucoid matter. There is salivary reservoir or receptacle in each gland which is an elongated sac like and thin-walled and store saliva.

Ducts from the two salivary glands joined to form a single common salivary duct. Likewise, ducts from two receptacle or reservoir joined to form a common duct of receptacle. Both common ducts join to form a common efferent salivary duct. It opens at base of hypopharynx (Refer Figure 1.21).

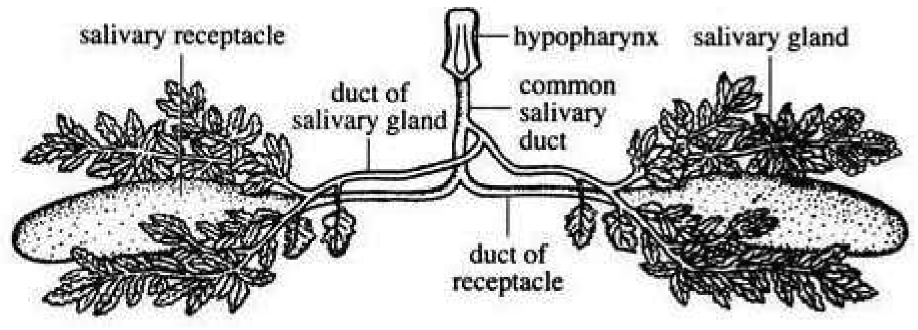


Fig. 1.21 *Salivary Apparatus of Cockroach*

Salivary Gland in Honey Bee

Digestive glands in honey bee are three pairs of salivary glands. Saliva from these glands mixes with pollens and nectar. Enzymatic action converts nectar into honey. It is either digested or regurgi-tated into comb for future use. Another pair of coiled glands is present in head of worker bees that produce nitrogenous food known as Royal jelly.

1.4.3 Digestion

Digestion is the chemical transformation of large and complex molecules in food to smaller molecules that can be absorbed through gut wall for insect nutrition. Digestion occurs mainly through enzymes, and physicochemical conditions particularly pH in insect gut. Digestive enzymes are basically present in saliva and gut.

Gut Enzymes: Digestion by intrinsic enzymes found mainly in midgut of most insects. Before ingestion, digestion of food is catalyzed by salivary enzymes. Microbial digestion is almost limited to hindgut. Proteinases, carbohydrases and lipases catalyzes the digestion of food containing protein, carbohydrates and lipids, respectively.

pH and Temperature: The crucial factors affecting digestion are temperature and pH. Enzymatic reactions increase with increasing temperature, from undetectable activity in cold conditions to a maximum, above which enzyme is gradually denatured and activity declines rapidly to zero. The pH of the gut varies throughout length of insect gut. In most insects the pH range is between 5.8 and 7.3, for example in the midgut of Locusta and other Orthoptera. pH of Lepidoptera (butterfly and moths) gut is always above 8 and can exceed 12 units.

Digestion of Macromolecules

Protein Digestion: The digestion of proteins involves endopeptidases, which attack peptide bonds within the protein molecule, and exopeptidases, which remove the terminal amino acids from the molecule. Insect groups vary in their composition of digestive proteases. For instance,

- In Coleoptera (for example, beetles), cysteine proteases are prevailing. The pH optimum of these enzymes, at 5-7 units, matches conditions in midgut of these insects.
- Larval Lepidoptera and several Diptera have serine proteases, specifically trypsin and chymotrypsin, which have a high pH optimum.
- Several insects have multiple proteases. Blood sucking insects (for example, mosquito) have 11 proteases, most of them are serine proteases that catalyze digestion of blood having complex of proteins.

Carbohydrate Digestion: Carbohydrates are generally absorbed as monosaccharides, for example glucose, fructose, etc. Thus, disaccharides and polysaccharides in food need digestion.

- Starch and glycogen are polysaccharides taken by insects from plants and animals, respectively. Starch and glycogen are digested by amylases that hydrolyze α-1,4-glucosidic linkages.
- Other common carbohydrases are α-glucosidases and β-glucosidases that hydrolyze particular disaccharides and oligosaccharides. For instance, sucrase (α -glucosidase) that breaks down sucrose in midgut of phloem sap-feeding aphids, β-galactosidase in digestive juice of palm weevil and a maltase (α-glucosidase) in the gut lumen of the larval housefly.
- Most potential carbohydrate for plant-feeding insects is cellulose, which is a β-1,4-glucose polymer. Cellulose is degraded by the combined action of three sets of enzymes namely endoglucanases, exoglucanases and β-glucosidases.

Lipid Digestion: The enzymes catalyze lipid digestion in insects are lipases. These enzymes cleave carboxyl ester linkages in Triacylglycerols (TAGs), Diacylglycerols (DAGs), galactolipids and phospholipids. Lipolysis occurs mainly in midgut and produces free fatty acids, glycerol, etc. that are absorbed into cells of midgut. Multiple lipases used in lipid digestion by some flies, butterflies, beetles and bugs. For example, lipid digestion in midgut of larval of an apple moth is catalyzed by six neutral lipases and three acidic lipases.

Digestion in Different Insects

I. Cockroach

Digestion of ingested food in cockroach occurs in following steps:

- Crushed food in mouth gets mixed with saliva secreted in salivarium. Mucus of saliva lubricates food, whereas zymase in saliva hydrolyses the starch material of food. Now lubricated and slightly digested food is propelled into pharynx from mouth by the help of labium.

- Food moves through alimentary canal by peristalsis that is a series of muscles contraction. Most part of digestion takes place in crop by action of saliva and digestive secretions from gastric cecae and midgut. After entering proventriculus, food undergoes further mastication through denticles that supported by longitudinal and annular muscles. Hair on pulvilli works as a filter that allows only smaller parts of food to move forward.
- In midgut, partially digested food is mixed with enzymatic secretions of epithelial cells of gastric ceaca and other secretory cells of midgut. These secretions have three categories of enzymes namely; i. trypsin like enzyme and peptidases which break down proteins, ii. amylase breaks the starch into glucose or fructose; and iii. lipase that breaks the fats.
- Peritrophic membrane of midgut protects its delicate lining from abrasion through hard indigestible parts of food. But it is permeable to enzymes and digested food. Thus, it does not block normal digestion of food and absorption of nutrients.

Absorption of Digested Food in Cockroach: Epithelial cells of gastric ceaca and other absorptive cells of midgut absorb the digested food. Absorbed food is stored in the diffuse fat bodies. Large amount of fat is absorbed by the epithelial cells of crop.

Egestion of Undigested Food in Cockroach: Undigested food is moved into ileum and then into colon. In rectum, first rectal pads absorb water and then faeces is eliminated outside as dry pellet though anus.

II. Honey Bee

Ingestion

Ingestion in honey bee occur in the following steps:

- It is process by which food is taken into gut. It involves food in mouth has lubrication and chemical effects from salivary and other glands. Swallowing of food sends it to midgut.
- Honey bee secrets enzymes to breakdown sugars within nectar it collects within mouth. Enzymes secreted from salivary gland and hypopharyngeal glands are sucrase, glucose oxidase and amylase.
- The nectar is swallowed via peristalsis and mixed or stored in crop. Food is filtered in crop via proventriculus and pollen removed from liquid. Pollen and other impurities are moved into midgut in form of a bolus.

Digestion

Digestion in honey bee occur in the following steps:

- Digestion starts in mouth with addition of enzymes from head glands. Most of chemical digestion occurs within midgut where digestive enzymes are secreted.
- Ingested food bolus is surrounded by peritrophic membrane that allows digestive enzymes to mix with food. Enzymes enter pollen via their pores and apertures and split proteins within into their amino acids. Digested food

moves through peritrophic membrane to epithelium to be absorbed into haemolymph.

- Assimilation is absorption of digested food into haemolymph for transport throughout body. Digested food has monosaccharides, amino acids and lipids. Passive absorption occurs via concentration gradients across epithelium enterocytes cells. Some absorption of foods minerals and water occurs in small intestine.

III. Housefly

- Liquified food premixed with saliva in pharynx and passes through esophagus either to crop or through proventriculus to midgut. Crop can contract to expel liquids in vomitus.
- Food materials enclosed in peritrophic membrane cannot be regurgitated. Large food particles and bacteria are restricted within peritrophic membrane through size exclusion. Digestion takes place in the lumen and small molecules move via peritrophic membrane to be absorbed by midgut epithelium.
- Ingested materials and waste pass posteriorly via midgut by peristalsis and join metabolic waste produced in Malpighian tubules.
- Water reabsorption takes place in hindgut and rectum. Faeces entry into the rectum is regulated by rectal valve. Rectal pads help in removing waste from rectum and water absorption.
- Epithelial cells of foregut and hindgut are protected from ingested bacteria by a cuticular lining. Thus throughout gut, bacteria ingested by adult houseflies are never in direct contact with epithelium.

Check Your Progress

11. What are sucking mouthparts?
12. What is trophallaxis?
13. Where salivary gland is located in cockroach?
14. How are carbohydrates absorbed in honey bees?

1.5 STRUCTURE AND PHYSIOLOGY OF RESPIRATORY ORGANS

Unlike vertebrates, insect respiratory system is separate from its circulatory system. Generally, in insects respiration occurs through tracheal system. Tracheal system is a complex network of tubes that supplies oxygen containing air to each part of insect body.

1.5.1 Respiratory Organs in Terrestrial Insects

As exoskeleton is impermeable in terrestrial insects respiratory gases move into insect body via a series of internal tubes known as tracheae or tracheal tubes. Thus, terrestrial insects have open respiratory system termed as tracheal system.

It consists of spiracles, tracheae and tracheoles through which metabolic gases are transported.

Following is the detailed structure of tracheal system of terrestrial insects:

i. Spiracles

Gases or air enter or leave insect body through small openings known as spiracles.

Number of Spiracles: The largest number of spiracles found in insects is ten pairs, two thoracic and eight abdominal; this occurs in dragonflies, grasshoppers, cockroaches, fleas and some bees and fly larvae.

Position of Spiracles: The spiracles are found on the thorax and abdomen and are lateral side in position. In abdomen of most insects they lie in soft membrane between terga and sterna.

Structure of Spiracles: It is a visible opening leads into a cavity called as atrium, from which tracheae arise. The walls of atrium are lined with fine hairs or filter apparatus that filter air as it enters to prevent the gas exchange system getting clogged (Refer Figure 1.22A). This is an adaptation to dry and dusty environments in which insects live. Spiracles have valves that can close in order to prevent water loss and regulate gas exchange. This closing mechanism occurs in spiracles of most terrestrial insects.

ii. Tracheae

The tracheae are larger tubes of tracheal system, running inward from spiracles and divided into finer branches, smallest branch of which are about 2 mm in diameter (Refer Figure 1.22C). Larger tracheae are multicellular forms, whereas smallest tracheae are just single cells. Generally, a pair of large diameter, longitudinal tracheae called lateral trunks run along length of insect internal to spiracles. Other longitudinal trunks are connected to heart, gut, and ventral nerve cord. Transverse commissures interconnect longitudinal tracheae and are generally one dorsal and another ventral, in each segment. Thus, tracheae are highly branched, thus increase surface area: volume ratio available for gas exchange. Tracheae are made from invaginations of ectoderm and thus lined by a cuticular lining called intima. Intima has outer epicuticle with a protein or chitin layer below it.

Taenidia: Surface of tracheal tubes is lined with a spiral thickening made of chitin called as taenidia (or chitin rings) (Refer Figure 1.22C). These chitin rings are strong but light in weight. Taenidia works as a supporting wire which keeps airways open during body movement, as well as gives flexibility during movement. This makes sure that surface of gas exchange is ventilated so that a concentration gradient is maintained.

iii. Tracheoles

At terminal of tracheal tubes, they undergo progressive subdivision to form a number of fine branches each 1 μ or lesser diameter called as tracheoles. Tracheoles are intracellular, enclosed within a very thin layer of cytoplasm from tracheoblast, i.e., tracheal end cell and penetrate throughout most tissues of insect body. They are particularly numerous in metabolically active tissues for example in flight muscles, fat body and testes.

Following are the advantages of tracheoles provided to insects:

- Much branched tracheoles provide an enormous surface area over which diffusion can occur.
- Tracheoles are so numerous that gaseous oxygen readily reaches most parts of insect body, as well as carbon dioxide easily diffuses out of tissues.
- End of tracheoles is filled with fluid. Respiratory gases can dissolve into this fluid and easily diffuse into nearby tissues as tracheoles have such thin walls.

iv. Air Sacs

In many insects, parts of tracheae are dilated or enlarged to increase reservoir of air. In some species dilations become **air sacs** (Refer Figure 1.22B). These air sacs collapse easily as taenidia of cuticular lining are reduced or absent. Sometimes volume of trachea can decrease within a developmental stage as air sacs are blocked by growing tissues. Air sacs are more developed in very active flying insects, for example bees and flies. They may assist flight by increasing buoyancy, but their main function is in ventilation of tracheal system.

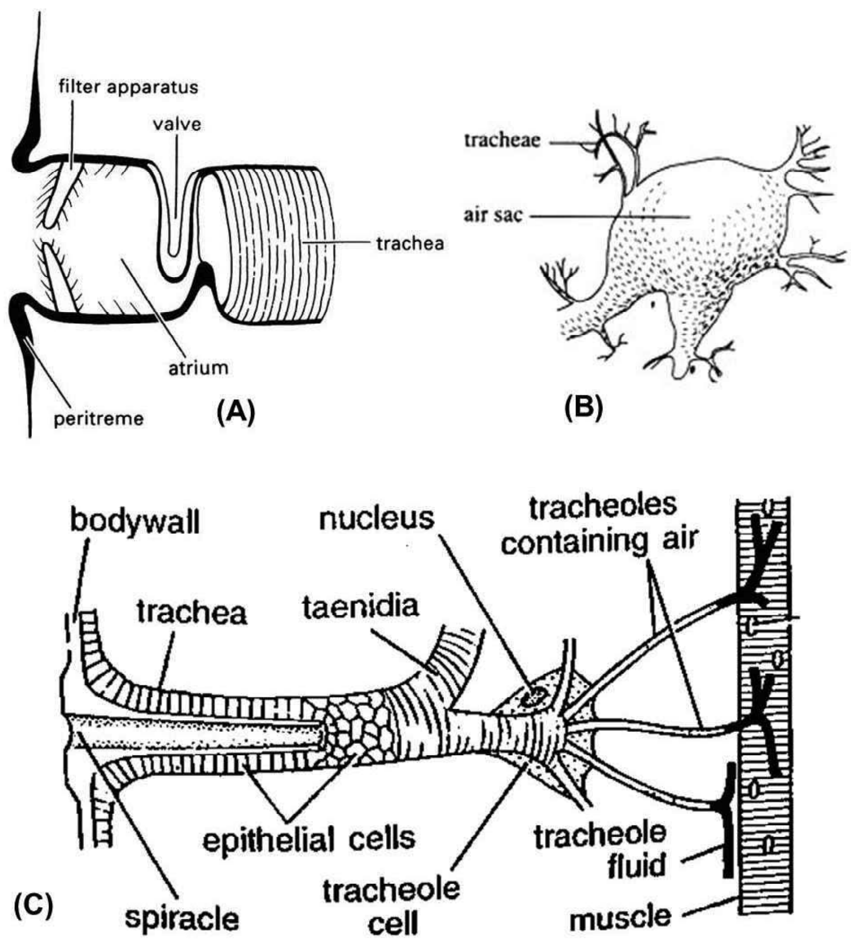


Fig. 1.22 *Structure of: A. Spiracle, B. Air Sac; and C. Tracheal System with Fluid Filled Tracheole at Rest in Cockroach*

Physiology of Respiration in Terrestrial Insects

In terrestrial insects, the air enters tracheal system by means of spiracles and is periodically changed through muscular movements as well as by diffusion. After each inspiratory act, spiracles are temporarily closed and first result of expiratory contraction is to push air enclosed in tracheae into its smallest branches. Then spiracles open and rest of respiratory movement is expended in driving CO_2, from the tracheae outside of body. Summary of respiration process is given in Figure 1.23.

Air enters insect's body through spiracles

↓

Air flow is regulated by muscles in valves of spiracle: contract to close spiracle or relax to open it

↓

Air moves to tracheal trunk and throughout tracheoles

↓

O_2 dissolves in fluid at ends of tracheoles

↓

Dissolved O_2 moves from high conc. in tracheole to a low conc. in cells by diffusion

↓

CO_2 produced as waste product of cellular respiration diffuses out of cell into tracheole

↓

CO_2 passes out of body through tracheal system & spiracles

Fig. 1.23 *Summary of Respiration Process*

Respiratory System of Different Terrestrial Insect

I. Cockroach

Respiratory system of cockroach is well developed to compensate the poorly developed circulatory system.

Respiratory Organs: As in other terrestrial insects, it has tracheae, tracheoles and spiracles (Refer Figure 1.24).

i. Tracheae

- It is a network of elastic, closed and branching air tubes lies in heamocoel. There are three pairs of large, parallel longitudinal tracheal trunks: one dorsal, one ventral and one lateral in position. All three pairs are joined together through transverse commissures.
- Tracheae are invaginations of outer integuments thus, they are formed from an outer epithelial layer lined by an inner chitinous cuticle. Cuticular lining is spirally thickened forming intima or taenidia. Taenidia helps to prevent tracheal tubes from collapsing.

- When cockroach is dissected under water, tracheae filled with air gives glistening appearance.

ii. Tracheoles

- The abundant branching tubes of tracheae connected with each other and penetrate to all over insect body. The finer branches of tracheae are known as tracheoles that connected with the each cell of body. Tracheoles have diameter of about 1μ.
- Their cavities are intracellular, that is each tracheole is made of a single cell. Wall of tracheole is very thin and lack cuticular lining instead its wall is lined by a protein trachein.
- Tracheoles are permeable to water. Their tips are filled with a fluid in which oxygen dissolves and diffuses to tissues.

iii. Spiracles

- The main tracheal trunks open outside body surface via small openings called spiracles or stigmata. Cockroach has ten pairs of segmentally arranged spiracles. Out of ten, two pairs of spiracles are thoracic, one located between pro- and mesothorax and the other between mesothorax and metathorax. Remaining eight pairs are abdominal, one pair in each of first eight segments of abdomen.
- Spiracles are located laterally in soft cuticle between terga and sterna. A spiracle guarded by bristles or hair that filters air to remove dirt. It is bordered by an annular sclerite called as **peritreme**.
- It has a closing mechanism as a simple valve that helps to prevent water loss. This valve can be closed or opened to regulate air flow.
- Spiracle has internal short tracheal chamber called atrium. Main tracheal trunk extends from this atrium.

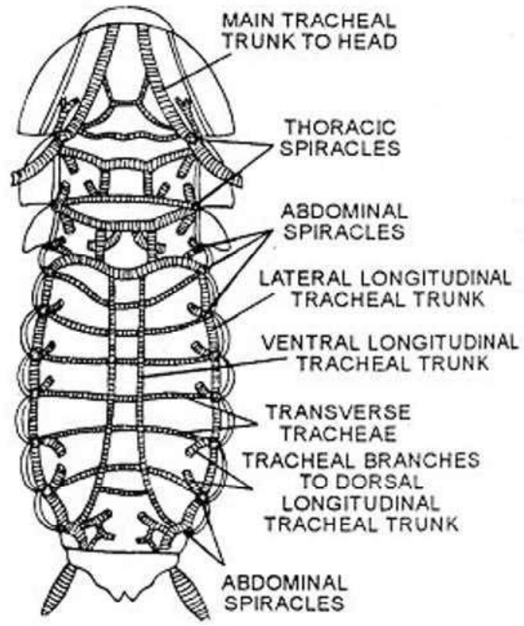


Fig. 1.24 *Respiratory Organs in Cockroach*

Respiratory Mechanism and Gaseous Exchange

Abdominal muscles also called **tergosternal muscles** of cockroach have alternate contraction and relaxation results in rhythmic contraction and expansions of abdomen. These movements lead to change in diameter of tracheae and push air in and out of tracheal tubes via spiracles. First and third pairs of spiracles are always opened whereas rest eight pairs of spiracles are only opened when inspiration occurs. Respiratory activities depend on insect activity and temperature. If there is more muscular activity, then faster is pumping air in and out of the insect body. Respiratory activities are coordinated and regulated by nerve centers located in thoracic ganglia. Nerve centers are stimulated through low concentration of Oxygen (O_2) and high concentration of Carbon Dioxide (CO_2) in tissue fluids.

Gaseous exchange takes place through diffusion between air in tracheae and dissolved gases in heamolymph or fluid of tracheoles. When cockroach rests, tip of each tracheole remain filled with fluid thus oxygen can diffuse slowly through fluid into cells of body. When metabolic activities are more, fluid from tracheoles is moved into neighboring tissue because of a rise in osmotic pressure of cells. This result in more surface walls of tracheoles exposed to O_2, to facilitate more oxygen to be provided to neighboring tissues. Oxygen moves into tissues leads to oxidation of energy rich food particles that produce energy, water and carbon dioxide. Some amount of CO_2 removed from body through tracheae and spiracles. But maximum concentration of CO_2 removed through cuticular lining of body as CO_2 can diffuse more easily through chitin than oxygen.

II. Honey Bee

Respiratory organs: Respiratory system of honey bee has spiracles, trachea, air sacs and tracheole (Refer Figure 1.26).

Spiracles: Both larva and adult bee have 10 pairs of spiracles on last two thoracic and first eight abdominal segments designated as from T2 – A8. The spiracle on T3 has valves that that open and close. T3 is smallest and A1 on propodeum (first abdominal segment of bees) is largest. Spiracle A8 is within sting chamber.

- **First Spiracle** on T2 has trachea connecting directly to spiracle membrane. The spiracle is hidden under a spiracle lobe which is lined with fine hairs. Spiracle has an external closing mechanism in which operculum, a sclerotized plate that does not fully cover opening. Operculum is controlled by occlusor (closing) muscle which connects to a small arm below spiracle membrane. When muscle contracts operculum closes over opening and when it relaxes the operculum opens (Refer Figure 1.25).
- **Second Spiracle** is small and permanently open.
- **Third Spiracle** on A1 (propodeum) has a long aperture of 0.23mm by 0.06mm when open. It is encircled by an elevated rim forming an external atrium. Within entrance to opening is controlled by two muscles occlusor attached to valve made up of soft integumental fold having strongly sclerotized margin. Contraction of occlusor (closing) muscle leads valve to move forward closing aperture. Relaxing of occlusor and contraction of dilator muscle makes valve to open aperture (Refer Figure 1.25).

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- **Abdominal Spiracle** has an internal atrium lined with filtering hairs. A domed shaped valve lies between atrium and trachea. Closing muscles move valve towards ridge and opening muscles pull valve away from ridge thus exposing trachea (Refer Figure 1.25).

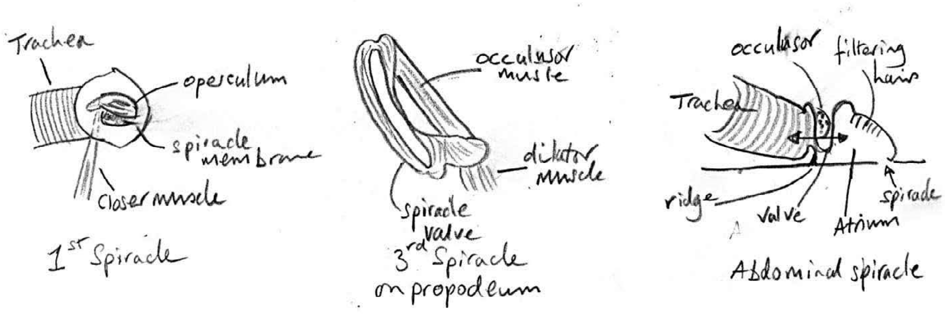

Fig.1.25 *Structure of Different Spiracles*

Trachea: It is made up of an outer epicuticle within sclerotized protein/chitin below it, a spiral thickening of intima runs along trachea, i.e., taenidia. Taenidia have protein/chitin that is sclerotized making strengthening mircofibrils.

Tracheoles: Tracheoles are blind-ended, air filled extensions of terminal tracheal cells. These are the main sites of gas exchange within bee. These are usually less than 2µm tapering to 0.3µm. Some tracheoles retain their cuticle after moulting unlike trachea. The single cell lining of tracheoles is very thin 16-20nm which gives a high surface to volume ratio which enables their high diffusion capacity.

Air Sacs: These are trachea without or limited taenidia. These are present throughout abdomen, thorax and head. This gives them ability to expand with air and collapse when empty. The air sacs provide a ready supply of oxygen to the brain and the muscles throughout body.

Respiratory Mechanisms: As respiration occurs in the cell, the products of respiration accumulate in the cell and this force the fluid in tracheoles to enter tissue. Exit of fluid creates low pressure in the tubes and draws in more oxygen to the tissues where it is needed. Other important facts are given in following points:

- During flight and high activity air is mainly drawn in through spiracle T2 and exhaled from T3. Abdominal spiracles are involved in intake of air during flight.
- Temperature affects breathing activity of honey bee. At 12°C there are no abdominal ventilatory movements. Above 28°C respiratory cycles are up to 100 per minute.
- When CO_2 is high the ganglia cause abdominal muscles to contract so as expelling the gas through spiracles and relaxing the muscles to allow oxygen in.

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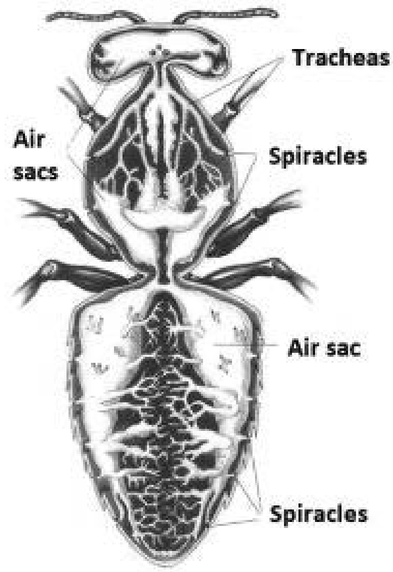

Fig. 1.26 *Respiratory System of Honey Bee*

1.5.2 Respiratory Organs in Aquatic Insects

Aquatic insects are equipped with a variety of adaptations that can supply oxygen under water or obtain it directly from their surroundings. There are basically two main groups of respiratory adaptations in aquatic insects namely closed and open tracheal systems (Refer Figure 1.27). Followings are the different means of closed and open tracheal systems through which different aquatic insects obtain oxygen and maintain their aquatic lifestyle.

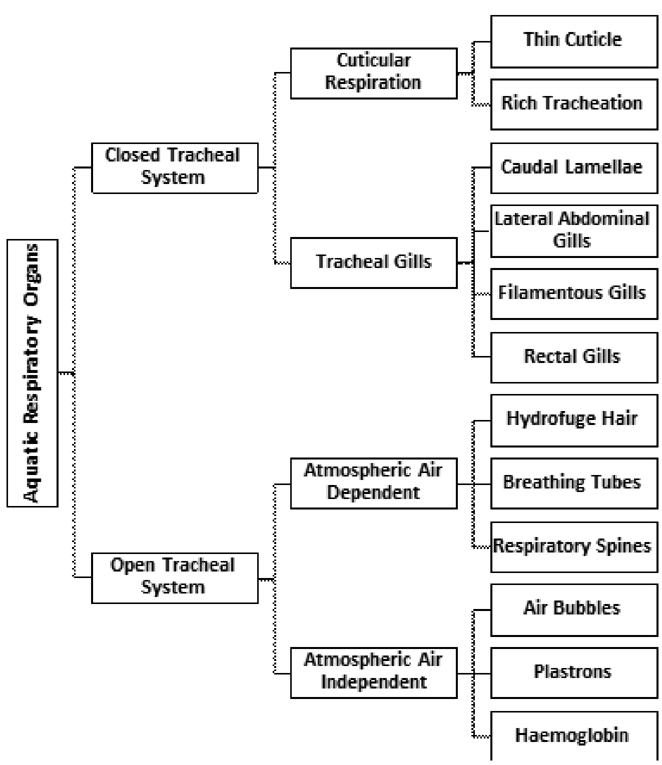

Fig. 1.27 *Components for Respiration or Gas Exchange in Aquatic Insects*

I. Closed Tracheal System

In this, all spiracles are sealed and non-functional, thus respiration takes place through body wall to tracheal system. Examples are cuticular respiration and tracheal gills.

i. Cuticular Respiration

Small aquatic insects or insects with low metabolic activity, respiration takes place through its body wall. Such insects have thinned cuticle, thus direct diffusion of gases, i.e., O_2 and CO_2 occurs through this exoskeleton into tracheal system. This type of respiratory system is called as cuticular or cutaneous respiration. Cuticular respiration can be sufficient to meet metabolic demands of small and inactive insects. These insects are living in cold, fast-moving streams where sufficient dissolved oxygen is present. Example is larvae of *Chironomus*.

In larger aquatic insects or insects with more active metabolism, all or part of body wall have very thin cuticle and rich tracheation immediately below their body wall. Therefore, leads to rapid entry and exit of gases, i.e., O_2 and CO_2 through exoskeleton in and out of tracheal system, respectively. This type of respiratory system is called as **cuticular respiration**. Example is Black flies.

Larger and more active aquatic insects or those living in oxygen deficient water may need to depend on other adaptations to complement cuticular respiration. Other adaptations are explained below:

ii. Tracheal Gills

Many aquatic larvae or insects have richly tracheated outgrowths of body wall collectively called as tracheal gills. They are covered by a thin layer of cuticle that is permeable to both oxygen and carbon dioxide. There are various forms of tracheal gills (Refer Figure 1.28) in different aquatic insects, these are followed:

- **Caudal Lamellae:** Larvae of Zygoptera have three caudal lamellae. The lamellae are also highly tracheated, and normally are major sites of gas exchange. The lamellae become especially important in oxygen deficient water. For example, in Coenagrion (genus of damselflies) up to 60% of oxygen uptake can occur through lamellae.
- **Lateral Abdominal Gills:** In mayflies and damselflies, the gills are paired, segmental and leaf or plate like structures located on sides or posterior end of abdomen. Larvae of mayflies live in oxygen deficient water, thus these gills are an important site of gas exchange. About 50% of an insect's oxygen demand is obtained by this way. Also, their rhythmic beating helps cuticular respiration by moving a current of water over their body. Fanning movements of gills keep them in contact with a constant supply of fresh water.
- **Filamentous Gills:** Stoneflies and caddisflies have filamentous gills found in tufts on various parts of body, such as thorax and abdomen.
- **Rectal Gills:** Dragonflies differ from other aquatic insects by having internal gills associated with rectum. Anterior part of rectum of larval dragonfly (suborder Anisoptera) is enlarged to become a branchial chamber whose walls have six rows of richly tracheated gills (Refer Figure 1.29). Water is

circulated in and out of rectum by anus due to muscular movements of abdomen. Rate of ventilation of branchial chamber depends on oxygen content of water and metabolic rate of insect. Cuticular respiration is perhaps not important in Anisoptera, whose body wall cuticle is usually thick.

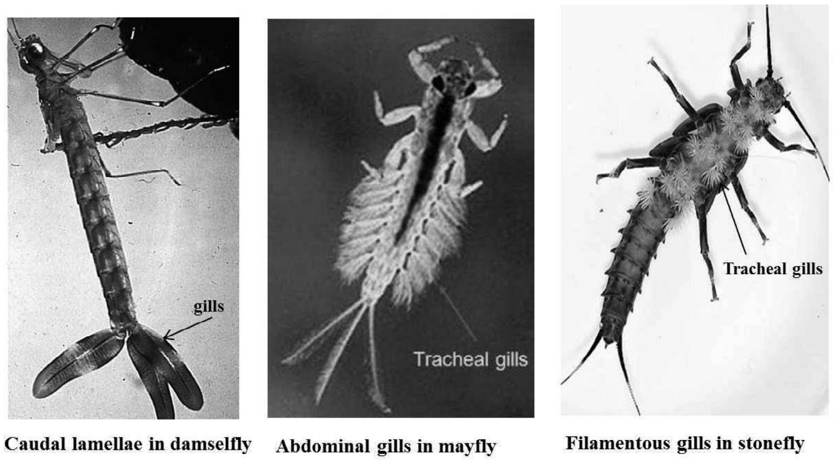

Fig. 1.28 *Different Tracheal Gills in Different Aquatic Insect Larvae*

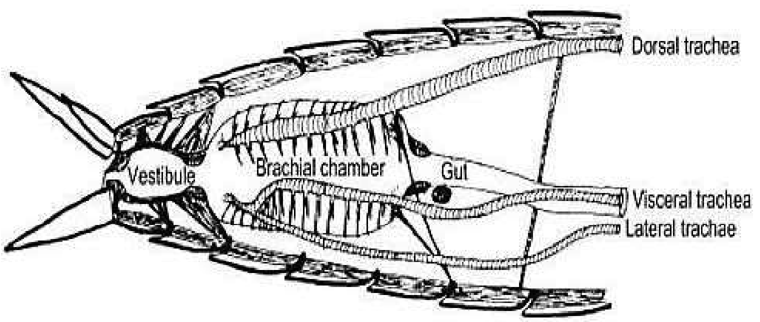

Fig.1.29 *Rectal Gills in Dragonfly Larvae, Longitudinal Section Shows Brachial Chamber*

II. Open Tracheal System: In this, some spiracles are functional, thus direct respiration takes place. Examples are air bubbles and plastron. Aquatic insects with open tracheal system can have two conditions, that are as follows:

- One condition is complete dependence on atmospheric air means that an insect have to frequently visit water surface for gas exchange in its tracheal system. Thus these insects are called as surface or atmospheric breathers. They have specialized structures around their spiracles, such as hydrofuge hair, breathing tube, etc.
- Second condition in which insect is completely independent of atmospheric air, i.e., where an insect maintains around its body a supply of atmospheric gas into which oxygen can diffuse from the surrounding water at a sufficient rate to totally satisfy insect's needs.

Atmospheric (Surface) Air Dependent: Aquatic insects always visit water surface to breath with the following respiratory structures,

i. **Hydrofuge Hair:** The spiracles of some aquatic insects are surrounded by special hairs called hydrofuge hairs. These hairs have a coating of waterproof wax. When insect submerged these hairs close over opening but when in

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contact with water surface they spread out to permit exchange of air (Refer Figure 1.30). Hydroguge hairs are important in preventing waterlogging of tracheal system when insects are submerged. These hairs also overcome surface tension force at air-water interface. Example are water scorpion and mosquito larvae.

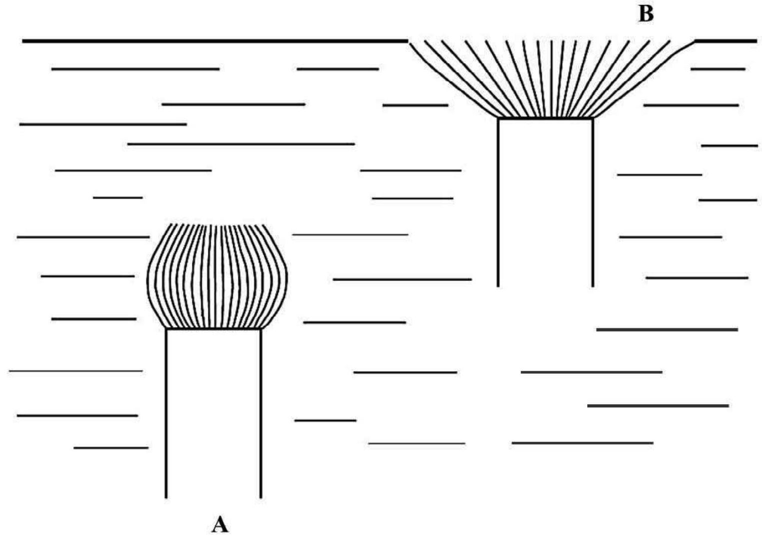

Fig. 1.30 *Hydrofuge Hairs*

In above Figure 1.30 hydrofuge hairs are shown, in which; A. shows when insect submerged, hair close over spiracle preventing entry of water; and B. shows when insect at surface of water, hairs separated by tension forces and spiracle exposed

ii. Breathing Tubes

Many aquatic insects get air straight from surface through hollow breathing tubes also called **siphons.** It works on same principle as a diver's snorkel. For example, in mosquito larvae and water scorpions, respiratory siphon tube is an extension of posterior spiracles (Refer Figure 1.31). An opening at end of siphon is surrounded by a ring of closely spaced hairs with a waterproof coating. At air-water interface, these hairs break surface tension of water and maintain an open airway. When insect dives, water pressure pushes hairs close together so they seal off opening and keep water out. In larvae of a syrphid fly the siphon is very extensible, its shape and flexibility giving its common name as rat-tailed maggots.

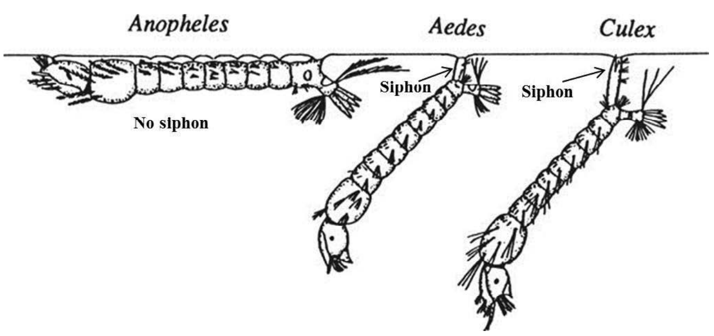

Fig.1.31 *Siphon in Mosquito Larvae, Anopheles Lack Siphon, Aedes has Short Siphon, and Culex has Long Slender Siphon*

iii. Respiratory Spines

The respiratory spines refer to extended shapes of posterior spiracles that can pierce tissues of aquatic plants to take oxygen. In a few species for example, larvae of *Mansonia* spp. mosquitoes live in mud, their siphon or posterior spiracle is rigid and pointed. They insert their spines into air stores made by aquatic plants (to maintain their buoyancy). Thus these insects obtain a rich supply of oxygen without moving to surface of water.

Atmospheric Air Independent: Some aquatic insects have breathing without dependence on atmospheric air or without moving to water surface through following methods,

i. Air Bubbles

Air bubbles are temporary air stores or gas stores (**compressible or physical gills**) which are common means of storing and extracting oxygen by some aquatic insects. Insects hold air bubble with their body when they dive below water surface. The bubble of stored air is in contact with spiracles by various means. For example, air bubble held under elytra (forewing) of adephagan water beetles and diving bugs (Refer Figure 1.32). Also, it can be trapped over some parts of body by fringes of hydrofuge hairs in some polyphagan water beetles. Generally, air bubble covers one or more spiracles so that insect can breathe air from bubble when submerged.

An air bubble provides an insect with temporary supply of oxygen, but these air bubbles also collect some oxygen dissolved in surrounding water. Thus bubble acts as a physical gill that refills its supply of oxygen through passive diffusion. An insect can remain under water as long as the volume of oxygen diffusing into air bubble. Size of bubble shrinks over time as nitrogen slowly diffuses out into water. When bubble's surface area decreases, its rate of gas exchange also decreases. Eventually, the bubble becomes too small to maintain metabolic demands of insects. Thus insect need renew air bubble by visiting again to water surface.

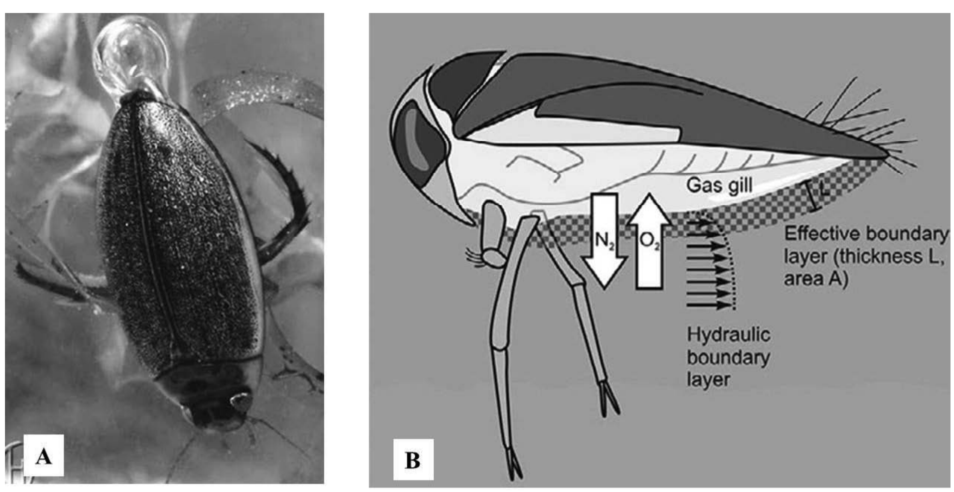

***Fig. 1.32** Air Bubble in Submerged: A. Water Beetle; and B. Water Bug has Gas Gill on its Ventral Surface*

In above Figure 1.32 the white arrows indicate direction of O_2 and N_2 diffusion between the bubble and the surrounding water through the boundary layer.

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ii. Plastrons

The thin film of air maintained on body surface which is connected with tracheal system through spiracles is called as **plastron**. Plastron is a further modification of air bubble that allows some aquatic insects to use permanent air stores also called as incompressible gill. Water is held away from body surface by hydrofuge hairs or a cuticular mesh, leaving a permanent gas or air layer in contact with spiracles. Cuticular extensions of body wall near to spiracles called as spiracular gills and found in aquatic pupa of some flies. Also, plastron held as a film around body by spiracular gills (Refer Figure1.33).

Air trapped within a plastron acts as a physical gill like air bubble but its volume remains constant. Thus, an insect's oxygen requirements can be fully satisfied by diffusion of oxygen into this gill. Insects that remain permanently submerged, for example riffle beetles or insects that do not able to reach water surface, for example eggs of floodwater mosquitoes have plastrons. These structures are visible underwater as thin, silvery films of air covering parts of body surface.

In these insects, volume of film or plastron is small as well as their respiration is slow. Thus, diffusion from surrounding water is enough to replenish oxygen in air plastron as fast as it is consumed. Because large amount of nitrogen from air dissolves in water slowly and maintains gas volume and support oxygen diffusion. Thus insects rarely need to renew their supply of air in plastron.

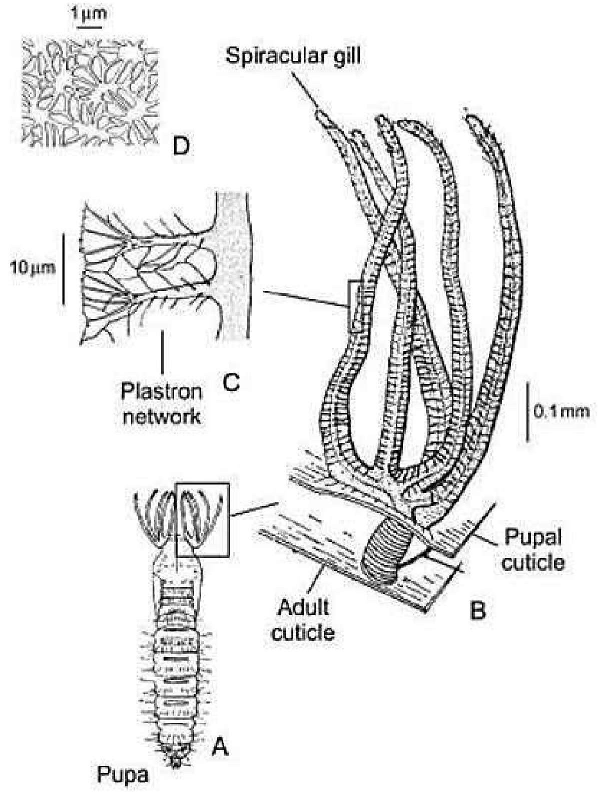

***Fig.1.33** Spiracular Gills of Blackfly Pupa*

Figure 1.33 shows spiracular gills of blackfly pupa in which A. shows their location on thorax, B shows the position of pupal cuticle relative to adult cuticle, C. shows the external plastron networks; and D. shows meshwork on surface.

iii. Haemoglobin

Haemoglobin is respiratory pigment that holds oxygen. It is an important component of all human red blood cells, but it is also found in a few insects. For example, larvae of some midges (genus *Chironomus*) called as bloodworms. These red colour worms live in muddy depths of ponds or streams where dissolved oxygen is in short supply. Hemoglobin molecules in blood bind and store oxygen. Whenever it is needed, oxygen is slowly released by hemoglobin for use by cells and tissues of insect body. This mechanism supply oxygen for very short term, but it is usually sufficient for insect that move into more oxygenated water.

1.5.3 Respiratory Organs in Parasitic Insects

Parasitic insects complete their development (life cycle) inside body of host animals usually other insect species. Thus, they are called endoparasitic insects, for example wasps in Hymenoptera. Endoparasitic insects get their oxygen supply directly from air outside the host or by diffusion through cuticle from surrounding host tissues. Followings are various means, through which gas exchange occurs in different endoparasitic insects:

i. **Cutaneous Diffusion**: It occurs in larval forms of parasitic wasps: Hymenoptera (for example, braconids and ichneumonids) and parasitic flies: Diptera (for example, cryptochetids) which parasitize scale insects. The spiracles of these endoparasites remain closed and non-functional until larvae mature and are about exit host body. Up to that time, these endoparasites are totally dependent upon cuticular diffusion of oxygen, either dissolved or gaseous, from host oxygen supplies. However, these larval forms have liquid-filled trachea in first instar and later instars have gas-filled trachea with closed spiracles and rich network of branches just below integument.

ii. **Caudal Vesicle:** The larvae of braconids have gas exchange by everting their hindgut through anus to form a caudal vesicle. It works as an additional surface for cuticular diffusion of oxygen from host tissues. Caudal vesicles are responsible for around one-third of total gas exchange. This is differently developed in different species of braconid wasps. In genus *Apanteles*, it is thin walled and connected with heart. Thus, when oxygen is passing in body, it is rapidly carried to all body parts (Refer Figure 1.34).

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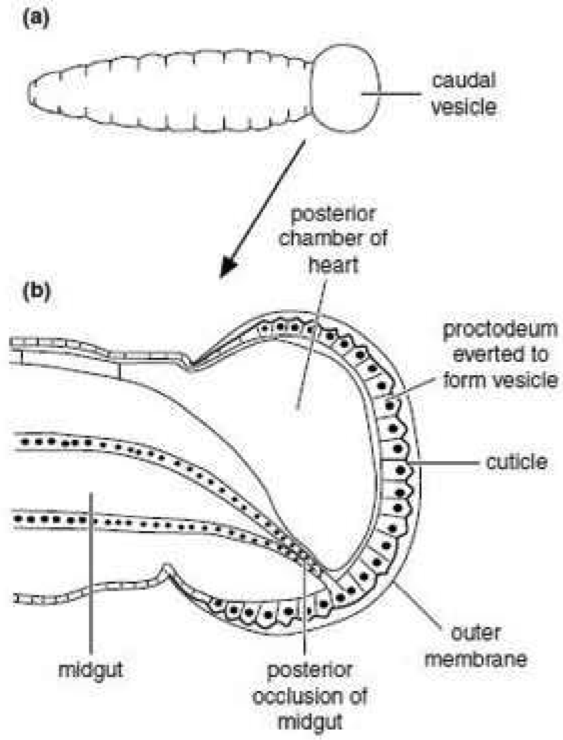

Fig.1.34 *Caudal Vesicle of Apanteles, Parasitic Wasp; A. Larva with Caudal Vesicle; and B. Longitudinal Section of Caudal Vesicle*

iii. **Caudal Filaments:** *Cryptochaetum iceryae* (dipteran parasite of scale insects) have two long caudal filaments. These caudal filaments in third instar larva are ten times as long as its body. Caudal filaments contain tracheae which become entangled with tracheae of its host. Atmospheric oxygen diffuses from host tracheae into tracheae contained in caudal filaments of parasite. Thus, it provides an easy path for oxygen transfer in this species of endoparasitic insect.

iv. **Egg Pedicel:** Endoparasites with greater oxygen requirements usually are in direct contact with atmospheric air either via the integument of the host or via the host's tracheal system. For example, larvae of many Chalcidoidea wasps have only posterior spiracles that are functional. These functional spiracles open into an air cavity formed at base of egg pedicel which pierces integument of host (Refer Figure 1.35A). Thus, larva attached posteriorly to remains of egg so that maintain contact with atmospheric air through the egg pedicel.

v. **Respiratory Funnel:** Larvae of several Tachinid flies (Dipteran Parasites) become enclosed in a respiratory funnel. Respiratory funnel is made by host when it is trying to encapsulate parasite (Refer Figure 1.35B). The funnel is formed due to inward growth of integument or tracheal wall of host. Within funnel, larva of Tachinid flies attaches itself by mouth hooks so that retaining contact with atmospheric air through entrance of funnel.

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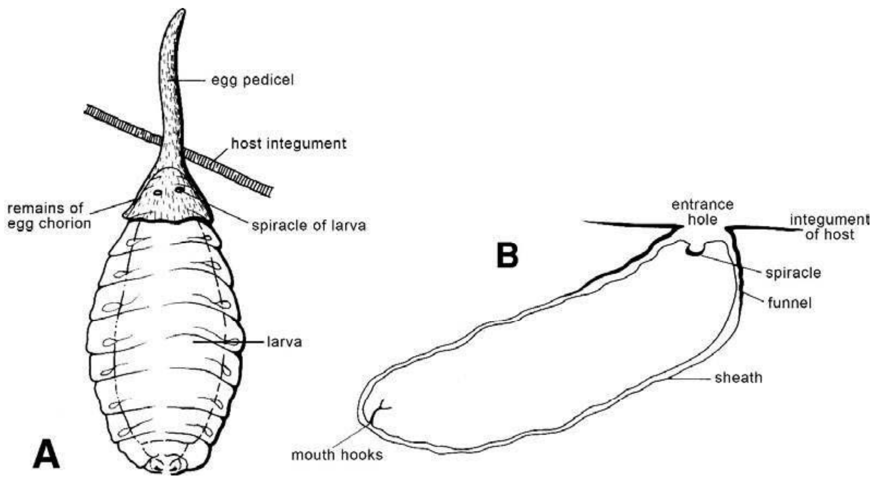

Fig. 1.35 *Respiratory Structures in Endoparasitic Insects*

In above Figure 1.35 respiratory structures in endoparasitic insects is shown in which; A. shows the larva of *Chalcidoid* Wasp (Hymenoptera) attached with egg pedicel; and B. shows the larva of Tachinid Flies (Diptera) with respiratory funnel formed by ingrowth of host's integument.

Check Your Progress

15. Define the term spiracles.
16. What are the total number of spiracles found in insects?
17. What are tracheal system?
18. What are plastrons?
19. What are tracheal gills?
20. Define the term siphons.

1.6 HAEMOLYMPH AND CIRCULATION IN INSECTS

Insects have open circulatory system that means fluid flows freely throughout body organs. An open circulatory system results from evolutionary development of haemocoel or body cavity. Due to open circulatory system, insects have only one extracellular fluid called **haemolymph** that serves functions of both blood and lymph of vertebrates. In insect, an open circulatory system has usually thin granular membranes separate tissues from haemolymph itself. Therefore, insects circulatory system have pumping structures and various diaphragms so that haemolymph flows within body cavity or haemocoel, reaching each body parts even most delicate appendages such as wings, antenna, etc. (Refer Figure 1.36).

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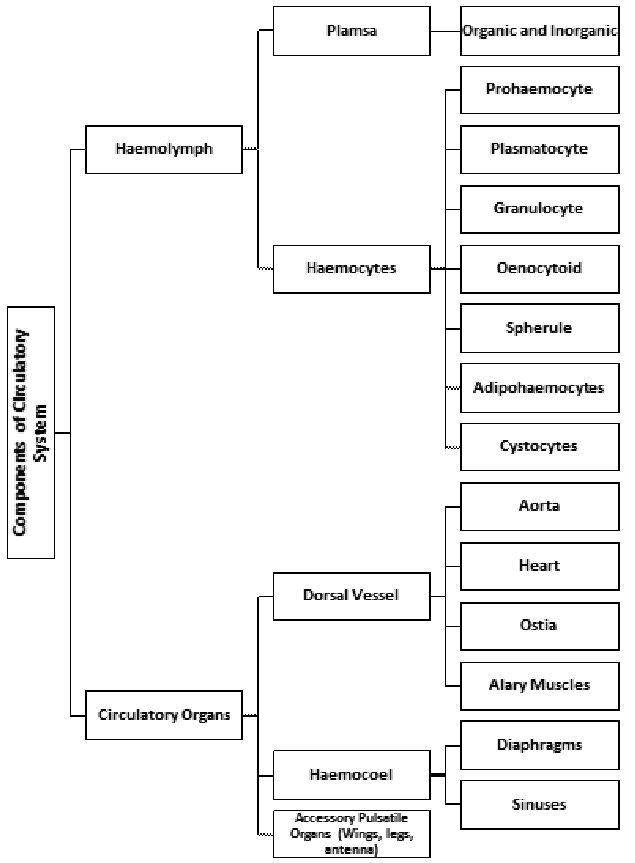

Fig. 1.36 *Components of Insect Circulatory System*

1.6.1 Structure and Function of Haemolymph

Haemolymph fills haemocoel and circulates around body, bathing the tissues directly. It contains fluid plasma in which nucleated cells, called as haemocytes, are suspended.

Physico-Chemical Properties of Haemolymph

Following are the physico-chemical properties of haemolymph:

- **Colour:** Haemolymph is generally colourless but is sometimes yellow or green. Some midges (blood worms) have hemoglobin in their blood and so heamolymph looks red.
- **pH:** The pH of insect haemolymph is generally between 6.4 and 6.8. Heamolymph with >7 pH units found in a dragonfly larva and in larvae of midge *Chironomus*.
- **Osmotic Pressure:** In many insects, haemolymph osmotic pressure is mostly constant over a range of environmental conditions. High haemolymph osmotic pressures occur in overwintering insects in diapause condition.

Plasma

Composition: Plasma has a large variety of organic and inorganic components. Amounts of both components vary among species as well as within an individual under different physiological conditions.

Inorganic Components

- In primitive and wingless insects, the predominant cation is sodium, with potassium, calcium, and magnesium present in low proportions. The major anion is chloride, though plasma also contains small amounts of phosphate and bicarbonate.
- In higher insect orders, relative importance of sodium decreases at the expense of potassium and, especially, magnesium. Chloride also decreases in importance and is replaced by organic anions, especially amino and carboxylic acids.
- Zoophagous species generally have a larger proportion of sodium in haemolymph, in contrast to phytophagous species where magnesium (derived from chlorophyll) and potassium are the major cations.
- The ionic composition may also change with stage of development. For example, in cockroach and locust, composition of haemolymph is similar in larvae and adults, because of their similar diet. While, in butterflies and bees, larval haemolymph has high magnesium, whereas adult haemolymph has higher sodium content.

Organic Components

Carboxylic Acids: These are important haemolymph constituents, particularly in larvae. These include citric, α-ketoglutaric, malic, fumaric, succinic, and oxaloacetic. Carboxylic acids are anionic, and thus may neutralize almost 50% of the inorganic cations. These are synthesized by insects or by symbiotic bacteria.

Amino Acids: Insects have high concentrations of amino acids in their haemolymph. The concentrations of amino acids vary among species and within an individual according to diet and developmental and physiological state. Amino acids are important in maintaining haemolymph osmotic pressure.

Protein: Plasma of insect haemolymph is protein rich. Protein concentration also increases through larval life, especially in the final instar, but then declines during pupation. Fat body is major source of many proteins found in haemolymph. Some protein in heamolymph, such as lysozyme, phenoloxidase, cecropins, and attacins are important for prevention of infection. Haemolymph of reproductive female insects contains high proportions of protein including vitellogenin. Vitellogenin is synthesized in fat body and transported via haemolymph to ovaries, where it is used by developing oocytes. Some plasma proteins work as transport agents for lipids and juvenile hormone.

Carbohydrate: Main carbohydrate in haemolymph of most insects is disaccharide trehalose that is a source of readily available energy. Glycerol and sorbitol are often found in high proportion in haemolymph of overwintering stages where these act as antifreezes.

Functions of Plasma

The plasma in haemolymph has following important functions:

- It acts as medium in which nutrients, hormones and waste products can be transported to body parts for its use, action, and removal, respectively in insects.

- It is an important site for temporary storage of metabolites.
- Plasma is a source of cell water. In desiccation condition, volume of plasma declines at the rate of water entering tissues.
- Being liquid, plasma is used to transmit pressure changes from one body part to another.
- It has an important role in thermoregulation of several actively flying insects.
- As it has organic and inorganic components, it is a strong buffer and resists changes in pH that can result from insect metabolism.

Haemocytes

Haemocytes are cells residing in haemolymph. In majority of insects, all or almost all of haemocytes are in circulation. But in some insects very few haemocytes circulate and majority of remaining loosely attached to surface of tissues. Haemocytes are generally measured as number of cells per unit haemolymph volume that is called as total haemocyte count. Total haemocyte count is greatly variable within same insect species and among different insect species. Insect has about 170 μl of haemolymph, the haemocytes counts range between 7 and 20 million circulating cells.

Types of Haemocytes

Various kinds of haemocytes are recognized that vary in size, stainability, function, and cytology (Refer Figure 1.37). Followings are details of different types of haemocytes:

- **Prohaemocyte**: Prohemocytes (stem cells) are small (10 μm or less in diameter), spherical or ellipsoidal cells whose nucleus occupy almost all cytoplasm. They usually undergo mitosis and are primary source of new haemocytes. As these are stem cells from which other kinds of haemocyte differentiate.
- **Plasmatocyte**: Plasmatocytes (phagocytes) are cells of variable shape and size, with a centrally placed, spherical nucleus surrounded by more vacuolated cytoplasm. Their cytoplasm have well-developed Golgi complex and endoplasmic reticulum, as well as many lysosomes. These cells have ability of amoeboid movement and are phagocytic.
- **Granulocyte**: Granulocytes are round or disc like in shape, with a small nucleus enclosed by cytoplasm filled with prominent granules. They are usually non-motile and involved in intermediary metabolism. On activation, granulocytes release granules. In some insects, they are amoeboid and phagocytic.
- **Oenocytoid:** Oenocytoids are spherical or ovoid cells having one or two, small and eccentric nuclei. They are nearly never phagocytic, as they lack lysosomes and have small Golgi complexes and poorly developed Endoplasmic Reticulum (ER). However, it is a non-adherent cell contains phenoloxidase activity.
- **Spherule:** Spherule cells are easily identifiable cells whose central nucleus is normally covered by mass of dense spherical inclusions occupying most of cytoplasm. These cells perform variety of functions such as phagocytosis, uptake and transport of materials, synthesis of certain blood proteins and in bacterial immunity.

- **Adipohaemocytes:** As their name suggest, adipohemocytes are cells whose cytoplasm usually has lipid droplets. Also, cytoplasm has non-lipid vacuoles and granules that contain carbohydrate material. These cells occasionally are phagocytic.
- **Cystocytes:** Cystocytes (coagulocytes) are spherical cells in whose small central nucleus. The chromatin is so arranged that nucleus look like cartwheel. Cytoplasm has granules that, when released from these fragile cells, that results in precipitation of nearby plasma. These cells have a major role in coagulation of haemolymph.

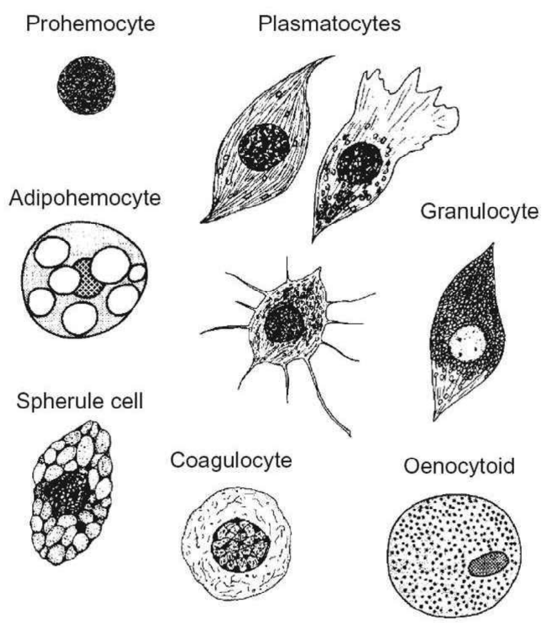

Fig. 1.37 *Types of Haemocytes*

Functions of Haemocytes

Haemocytes have a central role in development as well as in providing immunity. Detailed functions of heamocytes are given below:

- **Endocytosis:** It is a process through which a cell plasma membrane folds around any foreign or insect's own substance. Then this enclosed substance is ingested by cell without rupture of membrane. Endocytosis, particularly phagocytosis, is essential in both metamorphosis and defense against disease, as well as in regular elimination of dead or damaged cells.
- **Nodule Formation:** This process takes place when insect body is invaded by large numbers of particulate matter, such as bacterial aggregates and that cannot be eliminated effectively by phagocytosis.
- **Encapsulation:** Encapsulation is basically nodule formation on a larger scale. After invader is firstly coated with a thin layer of granulocytes or plasma proteins, layers of plasmatocytes enclose it. Encapsulation works as an insect's most important defense mechanism against endoparasites for example, nematodes and insects. Encapsulated organism almost always dies, as a result of starvation, deprivation of oxygen, and/or poisoning by quinones, antibacterial peptides, hydrogen peroxide and nitric oxide.

- **Identification of Foreign Matters and Altered Self:** Recognition of foreign matters or altered self is a main process in phagocytosis, nodule formation and encapsulation. For biological foreign matters, there are Pattern-Recognition Receptors (PRR) present both on surface of hemocytes and in plasma. As their name suggests, the PRR identify, then bind with particular molecular patterns on surface of foreign organism. They also identify altered self, particularly changes to basement membrane that covers all internal organs. This process is important during metamorphosis, when larval tissues are histolyzed, when an insect is injured and when microorganisms enter midgut epithelium.
- **Coagulation:** All forms of coagulation involve participation of coagulocyte. Coagulation begins when coagulocytes rupture, a stage which needs calcium ions. This releases haemocyte coagulogen, the cross-linking enzyme and microparticles.
- **Metabolic and Homeostatic Roles:** Haemocytes are essential for storage of nutrients and their distribution to growing tissues, formation of connective tissue, synthesis of chitin and maintenance of haemolymph sugar level. Certain haemocytes (spherule cells in flies, coenocytoids in other insects) have enzymes for metabolism of tyrosine, products of which are essential for tanning and/or darkening of cuticle.

1.6.2 Circulatory Organs

Haemolymph is circulated in each body parts via circulatory organs (Refer Figure 1.41). Detailed parts of insect circulatory organs are explained below:

i. Dorsal Vessel

The primary pump for moving haemolymph around the body is a middle dorsal vessel that runs entire length of insect body. Dorsal vessel is held in position by connective tissue attached to dorsal integument, tracheae, gut and other organs and via a series of paired fan-shaped alary muscles. Posterior part of vessel is called as heart and has valves known as **ostia**. While cephalothoracic that is anterior part of vessel and a simple tube known as **aorta**. Generally, the vessel is a straight tube, but in many insects the aorta can loop vertically. Usually, dorsal vessel is closed posteriorly. But in wingless and primitive insects, such as Diplura, dorsal vessel connects at its posterior end with arteries that run along cerci and caudal filament. In winged insects, circulation to appendages occurs by means of accessory pulsatile organs and septa. In most insects dorsal vessel is well tracheated. Histologically, dorsal vessel consists of a single layer of circular muscle fibers, sometimes longitudinal and oblique muscle layers also present.

Aorta and Heart: Generally, dorsal vessel is functionally bipartition into anterior aorta and posterior heart (Refer Figure 1.41A). The aorta is a narrow, simple tube and lacks incurrent ostia as well as alary muscles. Aorta is positioned ventrally to pass between corpora cardiaca and below brain. Aorta runs through thorax and into head, where haemolymph pours out into haemocoel. The posterior part, called as heart, is confined to abdomen. Heart has a wider luminal diameter, incurrent ostia, alary muscles, and a much thicker wall. Heart is the part that drives flow across the dorsal vessel. The heart may not be innervated or may receive paired lateral nerves from the brain and/or segmental ventral ganglia.

Ostia: Ostia can be simple, slit like valves or deep, funnel-shaped structures in wall of heart, or internal flaps (Refer Figure 1.38). Position and number of ostia also varies. They can be lateral, dorsal or ventral and can be as many as 12 pairs (in cockroaches) or as rare as 1 pair (in some dragonflies). Ostia are usually incurrent, that is, they open to allow haemolymph to enter heart but close to prevent backflow. But in some insects, such as crickets, some ostia are excurrent.

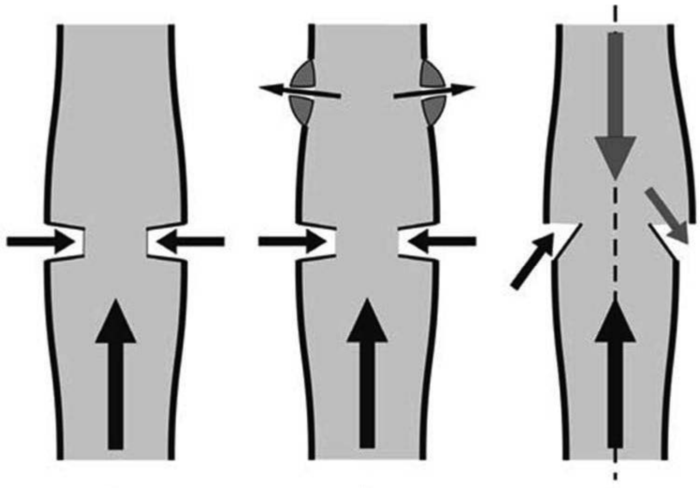

Fig. 1.38 *Diagrams of a Portion of Dorsal Vessel Showing Types of Ostia*

In above Figure 1.38 diagrams of a portion of dorsal vessel shows the types of ostia in which arrows indicate direction of haemolymph flow where A. shows the incurrent ostia with paired lips, B. shows incurrent ostia and excurrent ostia; and C. shows two-way ostia with a single (posterior) lip; left side (black arrow): incurrent flow during anterograde phase, right side (grey arrow): excurrent flow during retrograde phase.

ii. Haemocoel

Haemocoel is the body cavity of insects where heamolymph flows. The haemocoel of many insects has diaphragms and sinuses that are explained below as follows:

Diaphragms: Insects, particularly in their post larval stages, have various diaphragms or septa that help in directing flow of haemolymph. Diaphragms contain both connective tissue and muscular elements, such as alary muscle. Generally, insects have two horizontal diaphragms namely dorsal diaphragm and ventral diaphragm (Refer Figure 1.41B, C). The dorsal diaphragm (pericardial septum) lies immediately beneath the dorsal vessel and spreads between the alary muscles. Laterally, it is attached at intervals to terga and in most insects has openings so that pericardial sinus is in effect continuous with perivisceral sinus. A ventral diaphragm (perineural septum) can occur ventrally and separates perineural sinus from perivisceral sinus. Ventral diaphragm is usually limited to abdomen and present only in insects whose ventral nerve cord spreads into this part of body.

Sinuses: The spaces or chambers enclosed by diaphragms are known as sinuses. Generally, diaphragms subdivide heamocoel into three chambers or sinuses namely perivisceral, pericardial and perineural sinuses. The largest chamber known as perivisceral sinus is situated between dorsal diaphragm and ventral diaphragm. Pericardial sinus is situated above dorsal diaphragm and contains dorsal vessel. The perineural sinus is situated below ventral diaphragm and contains ventral nerve cord (Refer Figure 1.41B, C).

iii. Accessory Pulsatile Organs

Insects have various accessory pulsatile organs also called as **auxiliary hearts**. These help flow of haemolymph through insect appendages, for example wings, legs, antennae and ovipositor. In many insect, they are sac like structures which possess a posterior incurrent ostium and an anteriorly extended vessel. A pulsatile organ is found at base of each antenna. It has an ampulla from which a fine tube extends almost to tip of antenna (Refer Figure 1.40).

1.6.3 Mode of Circulation in Insects

Contractions of dorsal vessel and accessory pulsatile organs, along with movements of other internal organs cause flow of haemolymph around body. Generally, haemolymph is pumped quickly into dorsal vessel but moves slowly and discontinuously into sinuses and appendages.

i. Circulation in Haemocoel/Dorsal Vessel

Haemolymph circulation is maintained basically by dorsal vessel. Haemolymph is pumped forwards through heart at systole (contraction of heart), entering perivisceral sinus via anterior opening of aorta in head and/or via excurrent ostia of heart. The valves on incurrent ostia inhibit escape of haemolymph via these openings. Pressure of haemolymph leaving aorta anteriorly makes to flow haemolymph backwards in perivisceral sinus. Backwards flow is caused by the movements of dorsal diaphragm and by inflow of haemolymph into heart via incurrent ostia, at diastole (relaxation of heart muscle). Movements of ventral diaphragm assist to maintain supply of haemolymph to ventral nerve cord. The direction of haemolymph flow in most insects is indicated in (Refer Figure 1.39 and 1.42).

ii. Different Modes of Circulation

Different insect species have different modes of heamolymph circulation within dorsal vessel. Basically there are anterograde flow and retrograde flow of heamolymph.

- Primitive and wingless insects, for example mayflies have bidirectional flow of heamolymph. In this mode, a valve situated at posterior of dorsal vessel guard direction of haemolymph propulsion. Haemolymph anterior to valve is pushed toward head known as anterograde flow. Haemolymph posterior to valve is pushed toward posterior end of abdomen and into long caudal appendages called as retrograde flow.
- Many higher and winged insects for example, butterflies, beetles and flies, also involves heartbeat reversal. In heartbeat reversal, peristaltic waves of dorsal vessel periodically change direction. Usually periods of anterograde

and retrograde contractions are interrupted by a short stop and have different duration and contraction rates.

Mode of Circulation in Mosquito: During anterograde flow, haemolymph enters dorsal vessel via paired ostia in abdominal segments 2-7 and exits from dorsal vessel into head via an excurrent opening. During retrograde flow, haemolymph enters dorsal vessel via a pair of ostia at thoracic-abdominal junction and exits heart via a pair of excurrent openings at posterior end of heart or via two-way ostia (Refer Figure 1.39).

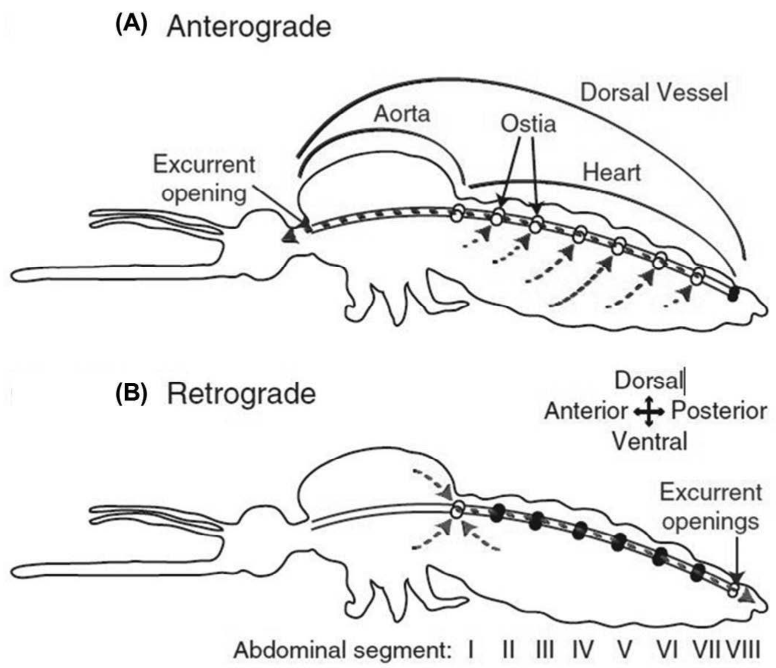

Fig. 1.39 *Mode of Haemolymph Circulation in Mosquito. L.S. of Mosquito During; A. Anterograde Heart Contraction Period; and B. Retrograde Heart Contraction Period*

Note: Flow of haemolymph is shown with dashed arrows.

iii. Circulation in Body Appendages

Insect appendages, such as antenna, wings, and legs are hollow, dead-end tubes filled with haemolymph. Due to their narrow openings, pumping activity of dorsal vessel does not cause flow of haemolymph into and out of these appendages. Diffusion also not works over such large distances. Thus, accessory pulsatile organs help exchange of haemolymph between haemocoel and appendages.

- **Antenna:** In head, antennae are supplied by specialized circulatory organs. In most insect, independent pumping organs in head are separate from dorsal vessel and supply haemolymph to antennae. These antennal hearts are consisting of muscle and basal ampulla to which antennal vessels are connected (Refer Figure 1.40A).
- **Leg:** Each leg of an insect contains a longitudinal diaphragm of connective tissue that subdivides leg haemocoel into two sinuses. The sinuses linked at tip of limb and have countercurrent haemolymph flow. Generally, haemolymph flow is driven by either periodic pumping of abdomen or by alternate twisting

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of elastic tracheal sacs that extend into leg (Refer Figure 1.40B).

- **Wings:** In most insects, complex interactions in dorsal vessel, accessory pulsatile organs in thorax, and elastic wing tracheae cause flow of haemolymph into and out of wing veins. In many insects such as butterflies, pulsatile organ has an arched muscular plate called pulsatile diaphragm which contracts independently from dorsal vessel (Refer Figure 1.40C).

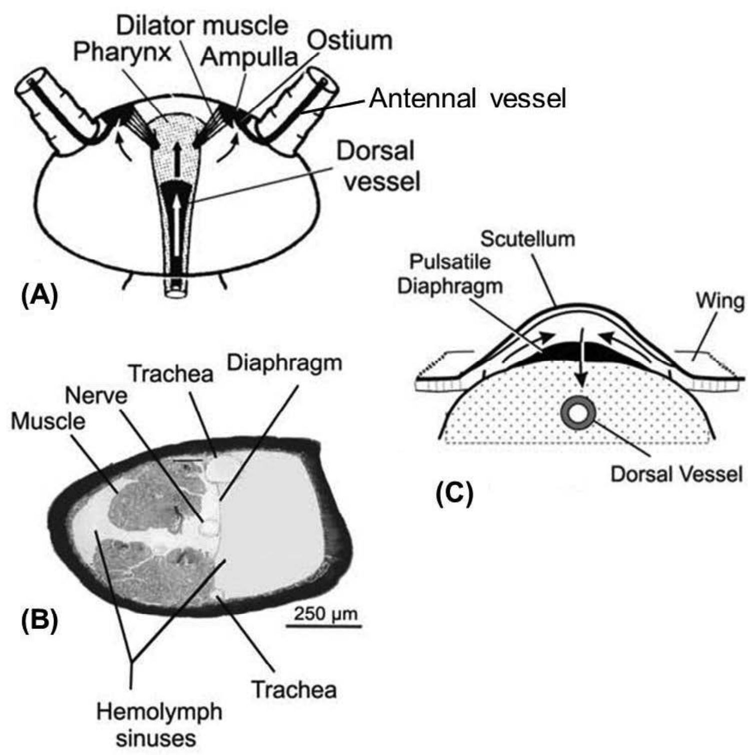

Fig. 1.40 *Accessory Pulsatile Organs of A. Antenna in Cricket, B. Leg in Cockroach; and C. Wing in Butterfly*

iv. Heartbeat

As in other animals, insect heartbeat involves contraction of heart (systole) followed by a phase of relaxation (diastole) and sometime a third phase diastasis follow diastole.

- **Systole:** It is contraction phase of heartbeat, caused by contractions of intrinsic muscles of heart wall. In most insects, having unidirectional flow of haemolymph, contraction of dorsal vessel starts at posterior end and spreads forward as a peristaltic wave.
- **Diastole:** It is expansion phase when haemolymph enters heart caused by relaxation of heart muscles. In most insects, Diastole is passive as occurs due to natural elasticity of the heart muscle. Generally, alary muscles are not responsible for diastole.
- **Diastasis:** After diastole there is a third phase in heartbeat cycle called as diastasis. Diastatis occurs when diameter of dorsal vessel or heart suddenly enlarges due to influx of haemolymph.

- **Heartbeat Rate:** Rate at which the heart beats varies greatly in different species and even within a species under different conditions. For example, pupa of Mediterranean flour moths has heartbeats at rate of 6–11 times per minute. Larval cockroach has rates of 180–310 heartbeats per minute. Usually, there is a decrease in heartbeat rate in successive larval or immature stages, and in pupal stage heart beats slowly or even stops to beat for long durations.

I. Circulatory System in Cockroach

As in most insects, circulatory system in cockroach is open type. In this, haemolymph flows freely within body cavity that is haemocoel. Circulatory system has heart and aorta but lack capillaries and veins.

i. Haemocoel

Body cavity or haemocoel (haima=blood, koila=cavity) is filled with blood called heamolymph.

- **Diaphragms:** Heamocoel is partitioned by dorsal and ventral diaphragm into three sinuses: i. dorsal pericardial, ii. middle perivisceral; and iii. ventral perineural (Refer Figure 1.41B,C). Diaphragms also have pores or fenestrae to allow flow blood from one sinus to another. Ventral diaphragm further extends into each leg as a septum dividing its cavity into two sinuses. One sinus is for outward and other sinus is for inward movement of heamolymph.
- **Dorsal Pericardial Sinus:** This sinus surrounds heart, aorta and paired fan-shaped (triangular) alary muscles. One pair in each segment, one on either side of heart. Apices of these muscles are attached to terga and their broad bases to dorsal diaphragm.
- **Perivisceral Sinus:** Middle or perivisceral sinus have alimentary canal. It has generally whitish mass of tissue or fat body. This sinus contains various types of cells. Trophocytes store reserve food in form of fat globules, protein globules and glycogen. Glycogen used during starvation. It has urate cells which are excretory in nature. Oenocytes in sinus synthesize wax whereas myocytes possess intracellular symbiotic bacteria.
- **Perineural Sinus:** Sternal or perineural sinus surrounds ventral nerve cord.

ii. Heart and Aorta

The heart is enclosed by dorsal pericardial sinus. It is positioned mid-dorsally below terga of thorax and abdomen. Heart is a long narrow tube having opened anterior end open and closed posterior end. It has 13 funnel shaped chambers or segments and each chamber are interconnected by a valve opening that usually in front of each segment (Refer Figure 1.41A). Bach end of each segment contain a pair of tiny lateral openings called as ostia. Ostia permits one directional flow of blood from pericardial sinus into heart only. Anterior part of heart is narrow and tubular called as anterior aorta. Anterior aorta has no ostia and forwards into head sinus.

iii. Heamolymph

Heamolymph or blood in cockroach has plasma and several types of cells called heamocytes. Its plasma is rich in amino acids, protein, uric acids and has some carbohydrate. Some cells of heamocytes transfer food material from blood to tissues while other cells act as phagocytes in eliminating metabolic wastes from tissues. Haemolymph has no respiratory pigments and thus does not help in respiration. Haemocytes counts ranges from 45,000–120,000 hemocytes/µl.

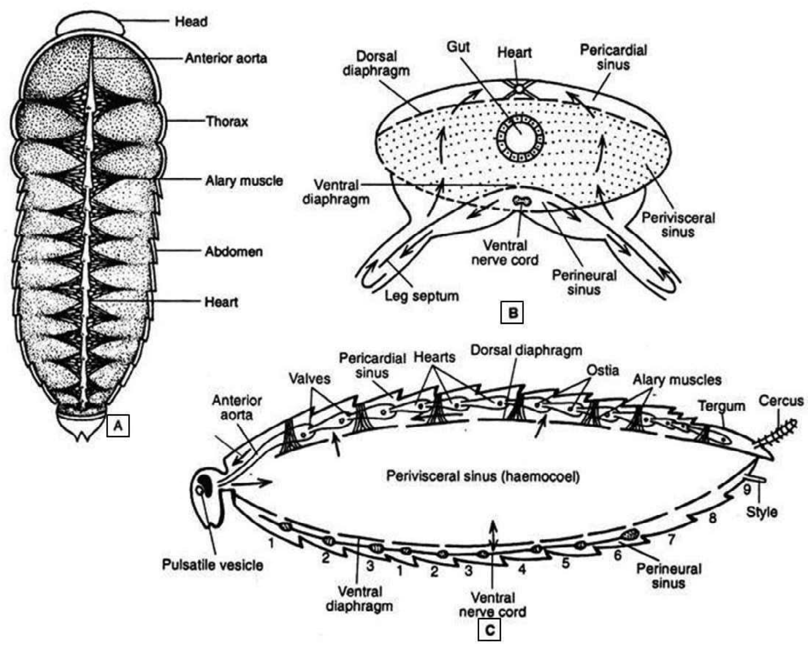

Fig. 1.41 *Circulatory System of Cockroach; A. Heart in Dorsal View, B. Heamolymph Circulation in T.S. of Thoracic Part, and C. Diaphragm and Sinuses in L.S. of body*

iv. Circulation Physiology

Heamolymph is circulated in heamocoel by contraction and relaxation of heart aided by alary muscles. Contraction of these muscles enlarges pericardial sinus so that blood flows into it from underlying perivisceral sinus. When muscles relax, blood is forced through ostia into heart (Refer Figure 1.42). Heart and aorta contract peristaltically from behind forwards driving blood into head sinuses and then backwards into perivisceral and sternal sinuses. The rate of heart beat in *Periplaneta* is 49 per minute.

From head sinuses, heamolymph is also sent into antennae by pumping activity of two small ampullae, located in head. In case of wings, small pulsatile organs at their bases assist in flow of heamolymph to fore and hindwings.

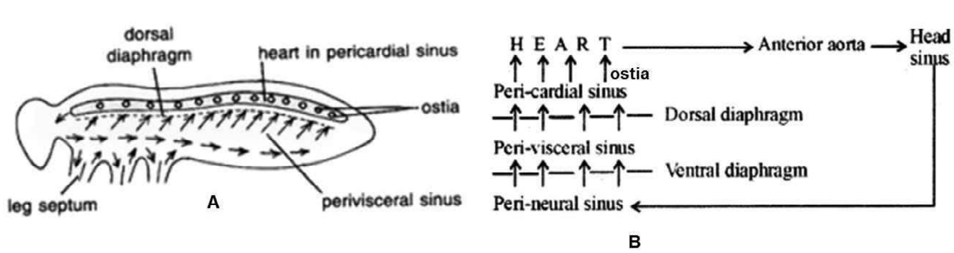

Fig. 1.42 *A. Circulation in L.S. of Body; and B. Schematic Representation of Blood Circulation in Cockroach*

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II. Honey Bee

Organs and Mode of Circulation: Circulatory system of honey bee consists of aorta, heart, dorsal, ventral diaphragms and antennal vesicle (Refer Figure 1.43).

- Circulatory system in honey bee is an open system. Haemolymph circulated around body though movements of diaphragms. Ventral diaphragm moves haemolymph from thorax. Dorsal diaphragm moves haemolymph forward within abdomen.
- Heart is closed at posterior and pumps haemolymph into aorta and towards brain. Heart contains 5 pairs of ostia which draw in haemolymph. Valves close when muscles forming walls of heart contract. This contraction forces haemolymph forward.
- The dorsal diaphragm connects at points from terga segments A3 through A6. It is transparent, contains muscle fibres and supports the heart. Above the diaphragm is the dorsal sinus. Movements in diaphragm move haemolymph forward in sinus creating current. A similar structure exists on the ventral side of abdomen. Ventral diaphragm starts in the thorax where it is attached to mesothorax and metathorax and ends as two long prongs attached to spiracle plates of segment A8.
- The aorta is a narrowing of heart that passes through petiole. It is coiled as it enters the thorax. Coiling is utilized for heat exchange between free flowing haemolymph and that within the aorta.
- Within head there is antennal vesicle which circulates haemolymph to antennae. The vesicle is non-muscular attached by tissue to muscles of pharynx. Similar structures are present at the bases of wings and legs to help in pumping haemolymph to these appendages.

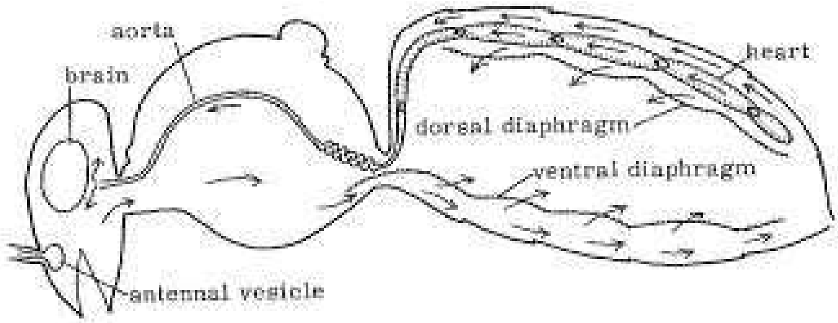

Fig. 1.43 *Circulatory System in Honey Bee*

Check Your Progress

21. What is the colour of haemolymph?
22. What is dorsal vessel?
23. List any three functions of plasma in haemolymph.
24. What are Oenocytoids?
25. What do you understand by accessory pulsatile organs?
26. Name different types of haemocytes.

1.7 EXCRETION IN INSECTS

Elimination of waste products of metabolism, mainly nitrogenous compounds from insect body is called as excretion. The process of excretion helps insect to maintain salt water balance and thus physiological homeostasis.

1.7.1 Excretory Organs

The process of excretion occurs through hindgut having Malpighian tubules, ileum and rectum. Following are the details about excretory organs:

i. Malpighian Tubules and Rectum

The Malpighian tubules and rectum work as a unit and form a major excretory system in most insects. Malpighian tubules are named after their discoverer, Marcelo Malpighi. They are long, thin, blindly ending tubules usually lie freely in haemocoel (body cavity) and open into alimentary canal at junction of midgut and hindgut. Usually they enter gut individually or they fuse first to form a common sac or ampulla or more tubular form ureter then enter into gut. They occur in almost all insects but are absent in springtails and aphids. Two-pronged bristletails have papillae (instead of Malpighian tubules) at junction of midgut and hindgut. Following are features and variations in forms of Malpighian tubules in insects,

- Number of Malpighian tubules varies from two from to several hundred, for example, 2 numbers in scale insects, 4 in bugs, 5 in mosquitoes, 6 in moths and butterflies, 60 in cockroach and around 250 in locusts. They also vary in length from 2 mm to 100 mm and in diameter from 30 mm to 100 mm.
- A tubule is made up of a single layer of epithelial cells, present on inner side of a basal lamina (Refer Figure 1.49). Each tubule is externally lined by peritoneal sheath and supplied with muscle fibres (helps in peristalsis) and tracheloes. They allow tubules to waving around in the haemolymph where they filter out solutes and helps in flow of fluid along tubules.
- The inner (apical) surface of cells modified into brush border also known as microvilli. The outer (basal) surface is also folded greatly. These features of cells facilitate the transport of materials and serve to increase greatly the surface area through which transport can occur.
- In many insects where tubules have only secretory function, histology of tubules is same throughout their length. Some insects, for example Rhodnius bugs, have tubules that are functionally differentiated into distal secretory region and proximal absorptive region.
- In beetles and larva of butterflies and moths, the distal parts of Malpighian tubules is closely connected to surface of rectum and enclosed within a perinephric membrane. This is called as a cryptonephridial arrangement of tubules. Cryptonephric tubules themselves are small, and near to fat body the epithelial cells are modified to form very thin windows called as leptophragmata (Refer Figure 1.44). This arrangement functions in improving reabsorption of water from material in rectum thus helps insects to adapt in very dry habitats.

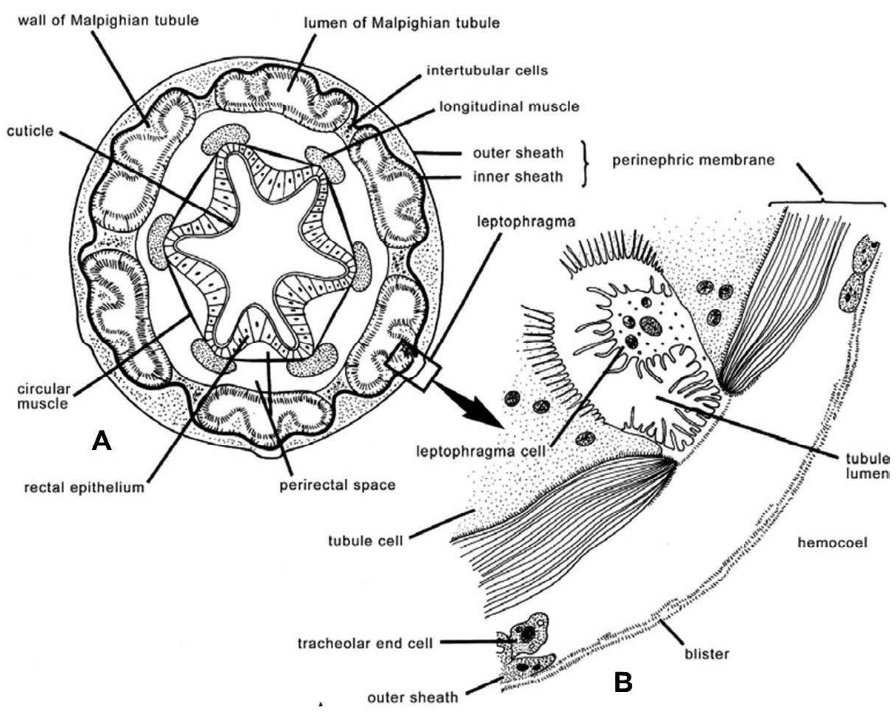

Fig.1.44 *Cryptonephridial Arrangement of Malpighian Tubules in a Beetle*

In above Figure 1.44 cryptonephridial arrangement of Malpighian tubules in a beetle is shown where; A. shows Cross section through posterior region of cryptonephridial part; and B. shows enlarged view of a leptophragma.

ii. Other Excretory Organs or Cells

In addition to Malpighian tubules, there are other cells and organs that functions in excretory system of insect.

- **Fat Body:** The fat body is groups of cells distributed throughout insect's body. Main role of these cells is to store food reserves, such as glycogen and fat, but they have also role in several metabolic activities. For example, they are involved in uric acid synthesis in many insects as the enzymes for uric acid synthesis perhaps present in fat body.
- **Urate Cells:** Some insects have urate cells that are scattered in the fat body. These highly specialized cells store uric acid during entire life of insect. As insect grows older, these cells become increasingly loaded with uric acid. For example, in cockroach much uric acid is stored in urate cells.
- **Nephrocytes:** Nephrocytes or pericardial cells are present singly or in groups in different parts of body. These cells can be very large (for example larvae of flies) or small. These are many in number and generally they have more than one nucleus. These generally are found on surface of the heart, or situated on pericardial septum or the alary muscles. These cells have a deeply invaginated plasma membrane which buds off pinosome into its internal cavity. These coalesce, crystallize, then the crystals are degraded and products enclosed in a large vacuole which is finally released into haemolymph. Thus, cells sieve haemolmph for products that they metabolize. This alters original waste material into a form that can be taken up by normal

metabolic pathways. Nephrocytes also take up dyes and probably colloidal particles from haemolymph.

1.7.2. Physiology of Excretion

In insects, most excretory materials are excreted into gut and eliminated within faecal matter. Excretion is also important in eliminating excess water and other unwanted chemicals that may be ingested and enter body fluids, for example plant toxic and excess salts. Also, main function of excretion is to eliminate excess nitrogen.

Forms of Nitrogenous Waste: Ammonia and uric acid are two main nitrogenous excretory products formed by insects. Insects produce very small amounts of urea.

- Ammonia is simplest form of waste, highly toxic and highly soluble in water. It is found as major excretory product in those insects that have available large amounts of water, for example, freshwater or aquatic insects. In addition to aquatic insects, larvae of meat-eating flies and cockroaches under some dietary conditions also produce ammonia. This kind of excretion is termed as ammonotelism.
- In terrestrial insects, water must be conserved, and more complex nitrogenous wastes are produced. Most insects, then, excrete their waste nitrogen as uric acid. This is slightly water-soluble, relatively non-toxic, and contains a smaller proportion of hydrogen compared with ammonia. Thus, it can be either retained in the body, or removed as a solid waste material with little water loss. This kind of excretion is termed as uricotelism.

Urine Production: A fluid is produced in Malpighian tubules to carry excreted materials to hindgut. This fluid is known as primary urine. Primary urine is different from excreta which are modified on its passage through the hindgut when it leaves insect via anus. Terrestrial insects that feed on solid foods they do not excrete completely liquid urine. Instead, it is mixed with undigested food in the rectum thus the faeces are more or less solid depending on quantity of urine it contains. But fluid-feeders and aquatic insects excrete liquid urine.

Physiology and Pathways of Excretion in Malpighian Tubules and Gut

Process and pathways of reabsorption, modification and excretion of materials through Malpighian tubules and gut are explained in following steps:

- Waste materials and excess water pass from haemolymph into Malpighian tubules, via crossing epithelial wall of these blind ended tubules.
- Removal of protons (H^+) from epithelial cell makes cytoplasm more negatively charged and also creates a concentration gradient (that is an electrochemical gradient). This attracts positive ions, for example Sodium (Na^+) and Potassium (K^+) into the cell from haemolymph. Influx of these positive ions drags in negative chloride ions to balance the charge. These ions move across the cytoplasm of cell, thus known as **transcellular pathway (Refer Figure 1.45)**.
- Certain small organic molecules are also actively transported into tubule lumen via transcellular pathway, including alkaloids (toxic plant

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compounds).Uric acid in a form of negatively charged urate ions is actively transported via transcellular pathway.

- The flux of ions across the epithelial cell also draws across water, via osmosis. This takes place mainly via the **paracellular pathway**, which is between epithelial cells **(Refer Figure 1.45)**. Sugars and amino acids are moved along via the water into tubule lumen.
- In proximal or lower part of tubule, uric acid is transported into tubule, against a concentration gradient and precipitates as crystals. These crystals are insoluble potassium urate formed when urate combines with high potassium content of tubule. These crystals form unevenly spherical masses in tubule lumen. Peristalsis moves these crystals into hindgut.
- In rectum, reabsorption of water and sodium and potassium ions takes place and the pH of the fluid decreases from 6.8-7.5 to 3.5-4.5. Useful organic molecules such as amino acids and sugars are also resorbed through the rectal wall.
- The combined effect of water reabsorption and pH change is to cause massive precipitation of urate. Remaining urate crystals excreted with faeces or urine via anus. Midgut is divided from hindgut via pyloric sphincter and when this sphincter is closed the hindgut takes only contents of Malpighian tubules.

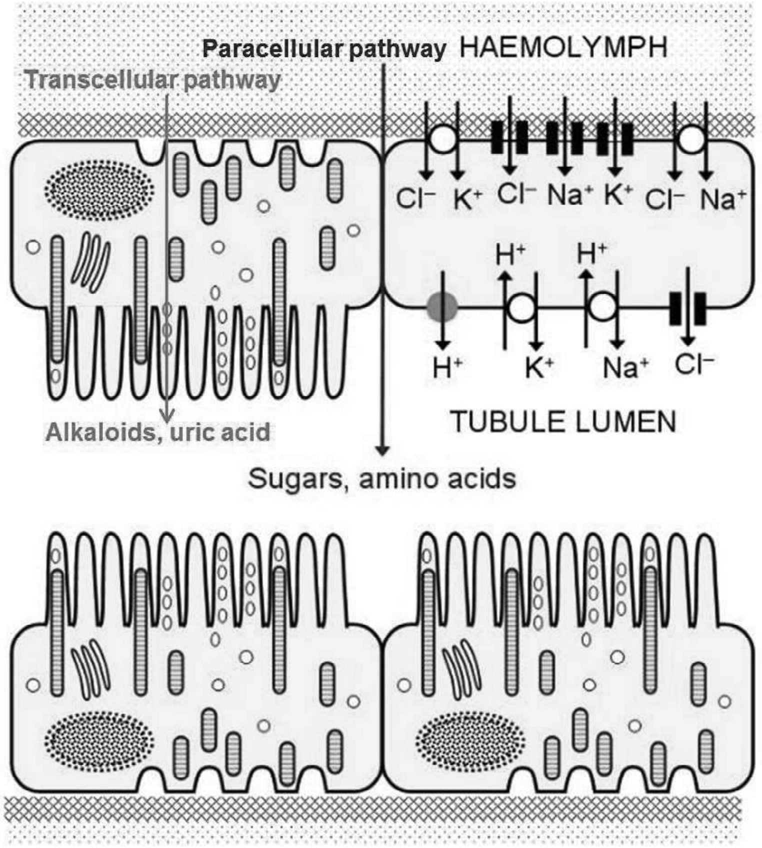

Fig. 1.45 Pathways of Movements and Reabsorption of Materials through Malpighian Tubules during Process of Excretion

Storage Excretion: In addition to excretion by Malpighian tubules, insects have **storage excretion** in which waste materials are stored safely and kept inside special storage cells. The excretory waste materials are retained within the body in different sites.

- Uric acid is stored as urates in the cells of fat body, for example American cockroach.
- Uric acid is stored in the body wall, giving white colour, for example Red cotton bug (*Dysdercus cingulatus*).
- Uric acid is stored in the male accessory glands to produce the outer coat of spermatophore or sperm ampulla, which is excreted during copulation.
- Uric acid is stored in the wing scales giving white colour, for example Pierid butterflies.
- Waste products of pupal metabolism (meconium) is stored and released during adult emergence.

1.7.3. Salt and Water Regulation in Insects

Salt and water balance is important for maintaining the haemolymph osmotic pressure. Regulation of salt and water content is dependent on nature of external environment. Insects in different habitats face different osmotic issues. These difficulties are generally overcome via same basic mechanism that is production of a primary excretory fluid or primary urine in the Malpighian tubules followed by selective reabsorption from or secretion into this fluid when it moves to rectum.

Before discussing about regulation of water and salts in insects of different habitats, some commonly used terminologies are as follows:

- **Osmosis:** It is movement of solvent molecules through a semipermeable membrane from a region having low solute concentration to a region having high solute concentration.
- **Osmotic Pressure:** It is the minimum pressure that must be applied to a solution to halt the flow of solvent molecules through a semipermeable membrane.
- **Isosmotic:** Solutions having equal osmotic pressure or condition in which total number of solutes, i.e., permeable and impermeable in a solution is equal to total solutes in another solution.
- **Isotonic:** It refers to a solution having same solute concentration as in a cell or a body fluid.
- **Hypertonic:** Solution with a higher solute concentration than that in another solution.
- **Hypotonic:** A solution that contains fewer dissolved particles (such as, salt and other electrolytes) than that in normal cells and blood.
- **Active Transport:** It is type of cellular transport in which materials (for example, ions, glucose, and amino acids) are transported across a biological membrane towards the region that already has a lot of these materials. Thus active transport uses chemical energy, i.e., ATP to move such materials against their concentration gradient.

- **Passive Transport:** Simple diffusion and osmosis are types of passive transport and do not require cell's ATP energy.
- **Diffusion:** It is movement of a molecule down a concentration gradient that is from an area of its high concentration to an area of its low concentration.

Terrestrial Insects

In terrestrial insects, the Malpighian tubules produce a fluid that is isosmotic with the haemolymph but of different ionic composition. Production of primary urine depends on the active movement of Potassium (K^+) or Sodium (Na^+) ions (cations) into Malpighian tubules followed by a passive movement of anions, primarily Chloride (Cl^-), to restore electrical equilibrium. The insect cannot normally sustain such a high loss of ions from haemolymph, and they are recovered by reabsorption from the fluid. Thus Malpighian tubules produces an isosmotic filtrate (urine) which is high in K^+ and low in Na^+ with Cl^- as major anion. The active transport of ions particularly K^+ into the tubule lumen creates an osmotic pressure gradient for passive flow of water. The continuous secretory activity of each Malpighian tubule leads to a flow of primary urine from its lumen towards and into the gut. In rectum, the urine is modified by removal of solutes and water to maintain fluid and ionic homeostasis of the body.

In most species, reabsorption occurs mainly in rectum, though the ileum also modifies fluid. In rectum major changes occur in osmotic pressure and composition of urine. Generally, urine becomes greatly hypertonic to haemolymph, but when much water is available a hypotonic fluid can be excreted. In rectum, water is reabsorbed against a concentration gradient that is active process uses cell energy. In Locusts, and in many other terrestrial insects eating solid food, this occurs in the ileum and the rectum and depends on the active reabsorption of chloride and sodium ions (Refer Figure 1.46). Potassium follows along the electrical potential gradient generated by the movement of chloride.

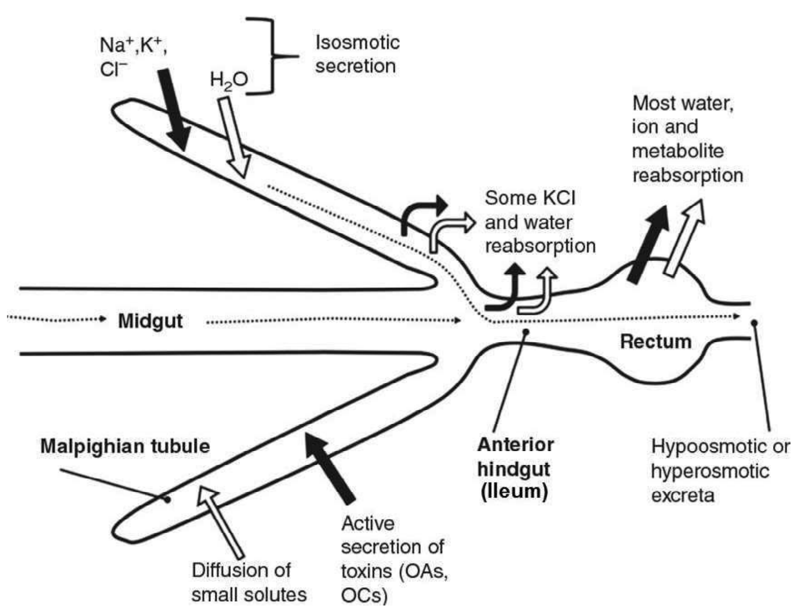

Fig. 1.46 *Schematic Diagram of the Insect Excretory System and Selective Reabsorption of Materials in a Terrestrial Insect (Locust)*

NOTES

In the above figure active transport is indicated by solid arrows and passive transport is indicated by open arrows. The flows of the gut contents and the fluid secreted by the Malpighian tubules are indicated by dashed arrows. Abbreviations used are as follows: OAs refers to Organic Anions: OAs and OCs refers to Organic Cations.

Freshwater Insects

Freshwater insects can regulate their haemolymph osmotic pressure successfully to point at which external environment becomes isosmotic with haemolymph. This is achieved by production of urine that is hypoosmotic to haemolymph. Beyond this point, regulation breaks down because freshwater insects are not able to produce hyperosmotic urine; that is, they cannot reabsorb water against a concentration gradient or excrete excess ions. Thus, they become osmoconformers, their haemolymph osmotic pressure closely paralleling that of external medium.

Freshwater insects are more likely to lose salts to the environment because most species have a highly permeable cuticle. Potassium, sodium and chloride are reabsorbed in the rectum, but water is not. Because of this, rectal fluid is hypotonic to haemolymph. Thus, salts are gained from food, but also from external environment by chloride cells.

Chloride Cells: Cells that absorb ions from or secrete them into surrounding medium are called as chloride cells. But they also transport other ions in addition to chloride. They have deeply folded plasma membrane, either at apical or basal surface and abundant mitochondria. The cuticle above the cell is also perforated.

In freshwater insects, food is common source of ions or salts that are absorbed via midgut wall. But, in some insects ions are accumulated via other parts of body. For example, salts are taken up by gills of caddisfly larvae, rectal gills of larval dragonfly, rectal chloride epithelium of damselfly and Mayfly larvae, anal gills of syrphid larvae and anal papillae of mosquito and midge larvae.

Role of Papillae in Salt and Water Regulation in Mosquitoes

Mosquito larvae have a pair of papillae that is located on each side of anus (Refer Figure 1.47A). These papillae communicate with haemocoel and are well supplied with tracheae. Their walls are a one cell thick syncytium and covered with a thin cuticle (Refer Figure 1.47B). Mosquito larvae can take chloride, sodium, potassium, and phosphate ions against large concentration gradients using papillae. The ability to accumulate ions varies with habitat in which an insect is normally found. Thus, *Culex pipiens* (common house mosquito), which is found in contaminated water, is less efficient in collecting ions than *Aedes aegypti* (yellow fever mosquito), which normally lives in fresh rainwater. Thus, larvae of *Aedes aegypti* are able to maintain their haemolymph osmotic pressure in a medium as they are able to take up salt from extremely dilute solutions.

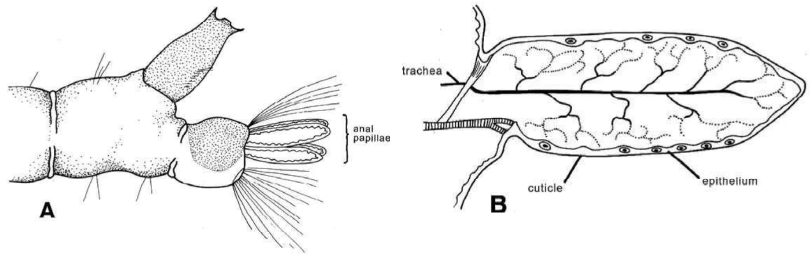

Fig. 1.47 *A. Posterior End of Mosquito Larvae (Aedes aegypti) with Anal Papillae; and (B) Structure of Anal Papilla*

Brackish-Water and Saltwater Insects

Brackish water is more saline (salt) than freshwater but less saline than seawater. Seawater or salt water is water from a sea or ocean and more saline than freshwater. Habitat occupied by brackish-water and saltwater insects vary largely in ionic content and osmotic pressure. During periods of warm and dry weather the salinity can increase many fold. After heavy rains or melting of snow in spring, salinity can be same as that of fresh water.

When their external medium is dilute that is its osmotic pressure is less than that of haemolymph, both brackish-water and saltwater insects osmoregulate to keep their haemolymph osmotic pressure more or less constant. Like freshwater species, they produce dilute urine and actively reabsorb salts via rectal wall. Mosquitoes from these habitats can accumulate ions via anal papillae. When external osmotic pressure rises above that of haemolymph, it leads to loss of water from body via osmosis. Thus, saltwater and brackish-water insects follow different strategies.

Role of Rectum in Salt and Water Regulation in Saltwater Mosquitoes

In saltwater mosquitoes, the Malpighian tubules produce a potassium rich fluid (primary urine) isosmotic with haemolymph and their main function is secretion of sulfate. Hyperosmotic urine produced as a result of active secretion of ions across rectum wall. Rectum in these insects is divided into anterior and posterior parts (Refer Figure 1.48). The posterior part is more important as it secretes sodium, chloride, magnesium, and potassium ions into rectal lumen. Role of anterior part is in exchange of bicarbonate for chloride ions and reabsorption of selected inorganic and organic solutes. Because of these activities, saltwater mosquitoes are able to strongly regulate their haemolymph osmotic pressure and ionic content over a wide range of external concentrations.

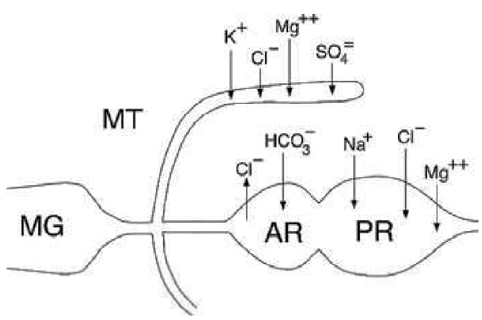

Fig. 1.48 *Excretory System of Saltwater Mosquito Larvae*

Note: Abbreviation used above are as follows: AR refers to Anterior Part of Rectum, MG refers to Midgut, MT refers to Malpighian Tubule and PR refers to Posterior Part of Rectum.

Excretory System in Different Insects

I. Cockroach

Excretory system regulates contents of nitrogenous material, inorganic salts and water in haemolymph. Protein metabolism results in excess production of nitrogen which is excreted as uric acid as in other terrestrial insects. The main organs and cells included in excretion process are: i. Malpighian tubules, ii. fat body cells, iii. uricose glands; and iv. cuticle.

i. Malpighian Tubules

Malpighian tubules are attached at anterior end of hindgut of the alimentary canal. These are fine, long, unbranched, yellowish and blind end tubules. These tubules are lying freely in haemolymph. Their number varies from 60 to 150 arranged in 6-8 bundles. Each tubule is about 16mm long and 0.5mm in diameter. Each tubule is lined by glandular epithelium having brush border (Refer Figure 1.49).

Tubule has two functional parts that is distal secretory and proximal absorptive parts (Refer Figure 1.50). Glandular cells of distal part extract nitrogenous waste in the form of uric acid salt also called **potassium urate** and water from haemolymph producing fluid called urine. The urine flows towards proximal part of tubule which reabsorbs some salts, for example potassium bicarbonate and water leads precipitation of uric acid. Uric acid present in haemolymph combines with reabsorbed potassium bicarbonate and water to form soluble potassium urate. Again this urate becomes available for actively transported from haemolymph into lumen of distal part of tubule. From tubule, uric acid moves into ileum via peristaltic waves. Some more water is reabsorbed in colon and rectum so that more or less solid urate is removed with faeces via anus.

ii. Fat Body Cells

Fat body is a lobed white tissue distributed throughout haemocoel. It has different kinds of cells but only urate cells are used for excretion purposes. These cells accumulate, produce and store uric acid as well as granules of urate throughout life. Thus, this process of excretion is also called as **storage excretion**.

iii. Uricose Glands

The mushroom gland of male cockroach contains long and blind end tubules at its periphery known as uricose glands or utriculi majors. These tubules store uric acid (storage excretion) and discharge it over spermatophore during copulation. So, these glands act as storage excretory organs between mating and as active excretory organs.

iv. Cuticle

Cuticle is also act as an area where nitrogenous waste material is accumulated and then removed with its shedding at each moult.

NOTES

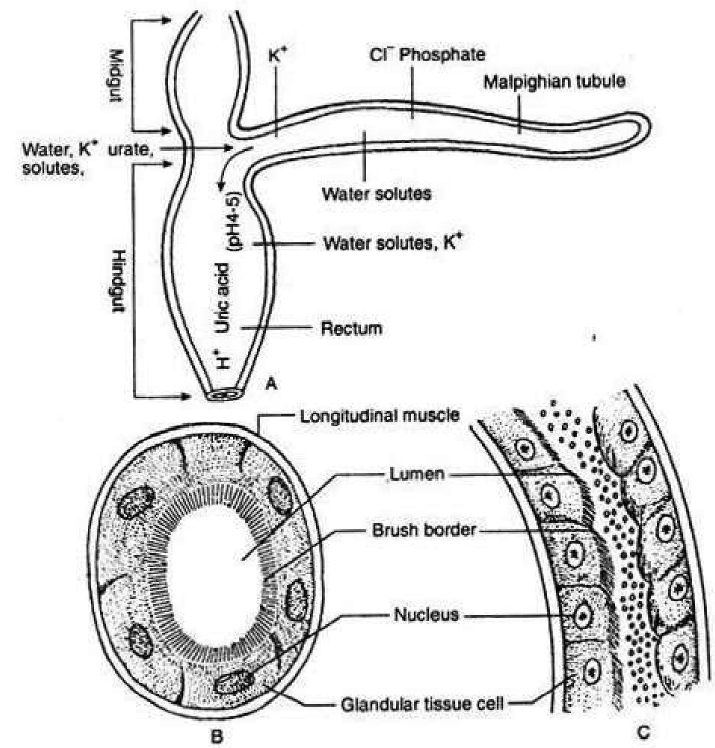

Fig. 1.49 *Malpighian Tubule of Cockroach; A. Location of Tubule, B. Transverse Section of Tubule; and C. Longitudinal Section of Tubule*

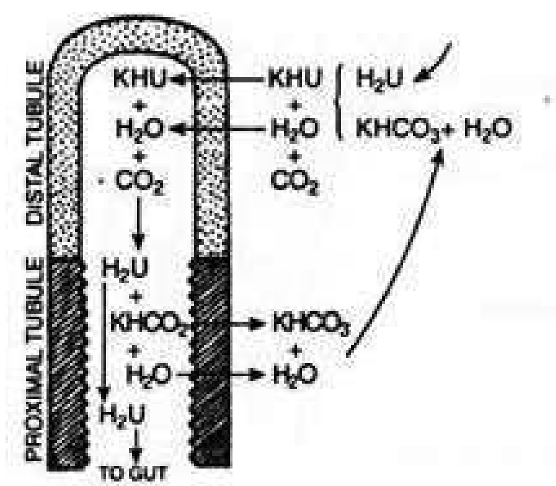

Fig.1.50 *Role of Different Parts of Tubule in Excretion*

Note: Abbreviations used above are as follows: H_2U refers to Uric Acid, KHU refers to Potassium Urate, $KHCO_3$ refers to Potassium Bicarbonate.

II. Honey Bee

- Waste products are collected from haemolymph by Malpighian tubules. Tubule has a single cell wall with an inner basal plasma membrane deeply infolded. The lumen of tubule has close packed microvilli. Tubule is surrounded by tracheoles and muscles.

- The tubule works through both passive filtration and active secretion from the heamolymph. Filtration occurs through the paracellular route (gaps between cells) and transcellular route (through cells). It is dependent on concentration gradients across the epithelium.
- Open end of tubule connects between midgut and pyloric valve where the uric acid from the tubule joins other waste, such as pollen husks from midgut and passes into small intestine.
- Some more absorption of water and minerals occurs in small intestine. Excreta is moved in to the rectum where it is stored. Excreta is evacuated as faeces by honey bee outside of hive.

Check Your Progress

27. Define the term excretion.
28. Why is excretion useful?
29. Name the excretory organ in insect.
30. What is primary urine?
31. Distinguish between hypertonic and hypotonic.
32. What are transcellular and paracellular pathways?
33. Define the term chloride cells.

1.8 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Insect cuticle is the outermost thick layer of integument secreted by epidermis.
2. Exocuticle is a dark pigmented, hard and sclerotized. It offers rigidity to the cuticle and consists of mainly chitin and a hard protein called sclerotin.
3. The insect cuticle is hard and forms unstretchable exoskeleton and it must be shed from time to time to permit the insects to increase their size during growth period. Before the old cuticle is shed new one has to be formed underneath it, this process is known as moulting.
4. Moulting is a complex process which accomplished in three steps: apolysis, ecdysis and sclerotization.
5. Oenocytes are named so because of their pale amber colour. These are considered as derivative of epidermal cells. Oenocytes are perhaps involved in lipid metabolism. They produce hydrocarbons including sex pheromones and other lipids that contribute to epicuticle. It is associated with the epidermis of the insect integument.
6. In insects, digestive system or alimentary canal is a tube of epithelium running from mouth to anus. The main role of alimentary canal is to process ingested food by mechanical and chemical means so insect can absorb nutrients for their growth and development.

7. The esophagus of some insects feeding on highly resinous plants bears single or paired diverticula, in which the resin is stored. For example, caterpillars of Myrascia, feed on Myrtaceae.
8. The midgut of Lepidoptera larvae has goblet cells, with a large flask-shaped central cavity. They play a role in regulation of the potassium level within haemolymph.
9. The functions of Peritrophic Membrane (PM) is as follows:
   - It prevent mechanical damage to midgut epithelium.
   - It prevent entry of microorganisms into body cavity.
   - Binds potential toxins and other damaging chemicals.
   - Divide midgut into an endoperitrophic space (between peritrophic envelope and midgut cells) and an ectoperitrophic space (in midgut lumen). This separation of epithelium increases digestion efficacy.
10. Many insects have finger like outgrowths at anterior end of midgut called as caeca (or gastric or hepatic or enteric caeca). Caeca is found in midgut of insects.
11. Sucking mouthparts are modified for piercing tissues of animals and plants to suck blood and plant juice. It is present in dipteran insects, for example mosquitoes and hemipteran insects like bugs, aphids, etc. This type of mouth arts is present in almost all the bloodsucking insects like tsetse fly, bed bug, etc.
12. The mutual or unilateral exchange of alimentary fluid, including saliva, is called trophallaxis. Oral transfer of regurgitated liquid from one adult to another is a typical feature of social Hymenoptera, for example wasps, and *Formica fusca* ants.
13. Salivary gland in cockroach is situated in thorax on either of dorso lateral sides of esophagus.
14. Carbohydrates are generally absorbed as monosaccharides in honey bees, for example glucose, fructose, etc. Thus, disaccharides and polysaccharides in food need digestion.
15. The spiracles are the external openings of the tracheal system, found on the thorax or abdomen. They are lateral in position, and in the insects there is one pair of spiracles on a segment, usually on the pleuron. Gases enter or leave the insect through these small openings.
16. The largest number of spiracles found in insects is ten pairs, two thoracic and eight abdominal; this occurs in dragonflies, grasshoppers, cockroaches, fleas and some bees and fly larvae.
17. The tracheae are larger tubes of tracheal system, running inward from spiracles and divided into finer branches, smallest branch of which are about 2 mm in diameter. Larger tracheae are multicellular forms, whereas smallest tracheae are just single cells. Generally, a pair of large diameter, longitudinal tracheae called lateral trunks run along length of insect internal to spiracles.

18. The thin film of air maintained on body surface which is connected with tracheal system through spiracles is called as plastron.
19. Many aquatic larvae or insects have richly tracheated outgrowths of body wall collectively called as tracheal gills.
20. Many aquatic insects get air straight from surface through hollow breathing tubes also called **siphons.**
21. Haemolymph is generally colourless but is sometimes yellow or green. Some midges (blood worms) have hemoglobin in their blood and so heamolymph looks red.
22. Dorsal vessel is a circulatory organ. The dorsal vessel is a cylindrical structure that extends the entire length of the insect and is organized by serial repetition of building blocks.
23. The plasma in haemolymph has following important functions:
    - It acts as medium in which nutrients, hormones and waste products can be transported to body parts for its use, action, and removal, respectively in insects.
    - It is an important site for temporary storage of metabolites.
    - Plasma is a source of cell water. In desiccation condition, volume of plasma declines at the rate of water entering tissues.
24. Oenocytoids are spherical or ovoid cells having one or two, small and eccentric nuclei. They are nearly never phagocytic, as they lack lysosomes and have small Golgi complexes and poorly developed Endoplasmic Reticulum (ER).
25. Insects have various accessory pulsatile organs also called as auxiliary hearts. These help flow of haemolymph through insect appendages, for example wings, legs, antennae and ovipositor.
26. Various kinds of haemocytes are as follows: prohemocytes, plasmatocytes, granulocytes, oenocytoids, spherule, adipohaemocytes and cystocytes.
27. Elimination of waste products of metabolism, mainly nitrogenous compounds from insect body is called as excretion.
28. The process of excretion helps insect to maintain salt water balance and thus physiological homeostasis.
29. The process of excretion occurs through hindgut having Malpighian tubules, ileum and rectum.
30. A fluid produced in Malpighian tubules to carry excreted materials to hindgut. This fluid is known as primary urine. Primary urine is different from excreta which are modified on its passage through the hindgut when it leaves insect via anus.
31. Solution with a higher solute concentration than that in another solution is called as hypertonic. Whereas a solution that contains fewer dissolved particles (such as, salt and other electrolytes) than that in normal cells and blood is known as hypotonic.

32. Movement of ions or salts through cytoplasm of epithelial cell in Malpighian tubule is known as **transcellular pathway.** Movement of ions or salt or sugar occurs between epithelial cells is known as **paracellular pathway**.
33. Cells that absorb ions from, or secrete them into surrounding medium are called as chloride cells.

1.9 SUMMARY

- The outermost layer of insect's body is called as integument or body wall.
- The integument mainly provides the outer shape of an insect and form exoskeleton, to which the muscles are attached.
- The body wall of insect integument consists of inner layer of cells called as the epidermis, and an outside covering called as the cuticle that lies on top of the epidermis.
- The epidermis lies on the basement membrane also called basal lamina.
- The basement membrane is the basal part of the body wall and seems like non-living shapeless granular layer.
- Epidermis is an inner unicellular layer below endocuticle and lying on basement membrane.
- Epidermal cells are polygonal type which transforms in to cuboidal or columnar during moulting.
- Epidermal cells are glandular and secrete cuticle and the enzymes involved in production and digestion of old cuticle during moulting. Thus, they have widespread Rough Endoplasmic Reticulum (RER) and Golgi complexes.
- Dermal glands produces a cement layer.
- Trichogen cells produce hair like seta or trichome.
- Moulting glands secrete moulting fluid which digests the old cuticle.
- Peristigmatic glands are found around the spiracles, for example in Dipteran larvae.
- Oenocytes are named so because of their pale amber colour. These are considered as derivative of epidermal cells.
- Cuticle is outermost thick layer of integument and is mainly produced from the cells of epidermis.
- A thick inner layer of cuticle is called the procuticle. It is made up of mainly chitin, proteins and other compounds.
- Chitin is a chief component of procuticle and thus contributes to excellent mechanical properties of cuticle.
- Exocuticle is outer layer, darkly pigmented, hard and sclerotized. It provides rigidity to cuticle and made up of chiefly chitin and a hard protein termed sclerotin.
- Endocuticle is inner layer, soft, light coloured and unsclerotized. It made up of more chitin but lacks hard protein sclerotin.

- Epicuticle is a thin outermost layer of cuticle and varies in thickness from 1-4μ. It provides the property of impermeability to entire cuticle. But it lacks chitin.
- Cement layer is produced from dermal glands and is made of lipoprotein. It protects the insect body from external harm.
- Wax layer is prominent layer and measures about 0.25μ approx. in thickness. It is made up of long chain of hydrocarbons, esters of fatty acids and alcohols.
- Polyphenol layer is a non-static layer having different kinds of phenols which are mainly used in the formation of the proteins.
- Polyphenol layer is resistant to acids and organic solvents thus provide protection from external chemicals.
- Cuticulin layer is an amber colour thin layer above epidermis and supported by outer polyphenol layer.
- Arthropodin is soft, untanned and water soluble protein found in endocuticle. The process of converting of arthropodin into sclerotin is referred as sclerotization or tanning.
- Sclerotin is amber coloured tanned cuticular protein and found only in exocuticle. This protein is insoluble in water.
- Resilin is a colourless elastic cuticular protein provides flexibility to sclerites, for example, wing articulatory sclerites.
- Colour of an insect depends on integument. Integument has various pigment molecules called chomophores which gives characteristic colours to different insects.
- Cuticle is a thick hard and brown coloured. It covers externally whole body of cockroach including appendages.
- Epidermis is situated below cuticle that it secretes. It is highly organized and has columnar cells arranged in single layer. It rests on basement membrane and anchored into by hemidesmosomes.
- Before the old cuticle is removed new cuticle has to be made below it, this process is called as moulting.
- Moulting takes place many times in an insect during the immature stages before becoming adult.
- The time interval between the two succeeding moulting is known as stadium and the stage formed by the insect in a stadium is known as instar.
- The dissolution of old cuticle and formation of new cuticle is known as apolysis.
- The process of the actual shedding of the old cuticle is called as ecdysis.
- Any kind of line or narrow space separating sclerotic areas of cuticle is called a suture. Sutures are flexible lines of integument between sclerites.
- In insects, digestive system or alimentary canal is a tube of epithelium running from mouth to anus.

- The main role of alimentary canal is to process ingested food by mechanical and chemical means so insect can absorb nutrients for their growth and development.
- The alimentary canal of insects has three main parts, i.e., foregut (or stomodeum), midgut (or mesenteron) and hindgut (or proctodeum).
- The alimentary canal is also commonly called as gut.
- All parts of insect gut are made of single layer of epithelial cells, bounded by basement membrane and striated muscle.
- The foregut and hindgut are ectodermal in origin, whereas midgut has endodermal origin.
- Cells of foregut and hindgut secrete cuticle.
- The cuticle lining of foregut and hindgut is known as intima.
- Foregut (or stomodeum) is the anterior part of alimentary canal. In foregut, the food can be stored, filtered, and partly digested.
- The cells of foregut are flattened and undifferentiated as they are not usually involved in absorption or secretion.
- The esophagus or oesophagus is a simple tube connecting the pharynx and crop. It serves to pass food back from the pharynx to the crop.
- The crop is a storage organ is an extensible part of foregut just after the esophagus. During storage the food undergo some digestion in insects whose saliva contains enzymes or that regurgitate digestive fluid from midgut.
- The midgut also called ventriculusis the middle section of alimentary canal.
- Midgut is of endodermal origin and, thus has no cuticular lining.
- The cells of midgut serve to secrete digestive enzymes or juices and to absorb the nutrients from digestion of food.
- Major cells of internal lining of midgut are tall and columnar cells and the membrane extended into numerous small, villi like folds called microvilli.
- Many insects have finger like outgrowths at anterior end of midgut called as caeca.
- The beginning of the hindgut is usually marked by pyloric valve and insertion of the Malpighian tubules.
- The rectum is most posterior part of hindgut and is an enlarged sac. It has thin epithelial wall except for some areas where rectum has 6-8 rectal pads that are thick-walled and radially arranged.
- In cockroach, alimentary canal is a long and coiled tube of uneven diameter. It has three regions as in other insects, i.e., foregut, midgut and hindgut.
- The middle part of alimentary canal is the midgut which is short and narrow tube. Inside wall of midgut is made up of glandular epithelium.
- Midgut works as true stomach and serves in digestion of food and absorption of nutrients.

- Phytophagous insects feed on plants and these insects mainly belong to orders, such as Orthoptera, Lepidoptera, Homoptera, Thysanoptera, Phasmida, Isoptera, Coleoptera, Hymenoptera and some Diptera. Phytophagous insects are also called herbivores.
- Insect predators eat basically other insects and are belong to orders Odonata, Mantodea, Heteroptera, Mecoptera, Diptera, Coleoptera, and Hymenoptera.
- Saprophagous insects are scavengers as they feed on dead or decaying plant and animal tissues. These insects belong to many orders, such as Blattodea, Isoptera, Coleoptera, and Diptera.
- A parasitic insect feed and complete its development in one host that may be other insect species or other animals.
- Amino acids are used for synthesis of proteins and enzymes for transport and storage, and as receptor molecules.
- The labrum is a broad lobe attached to clypeus in front of mouth. Labrum is also called as upper lip. On its inner side it is membranous and has some gustatory sensilla. Labrum helps in tasting and also handling the food.
- Mandibles are a pair of triangular, hard, unjointed, stout, chitinised structures.
- The maxillae occupy a lateral position, one on each side of head behind mandibles.
- The hypopharynx is a median lobe immediately behind the mouth. It is chitinous, grooved and a rod-like structure and hanging into preoral cavity. It is also called as tongue.
- The mandibles are a pair of jaws attached to head. Insect uses them to chew wood when restructuring the hive entrance, to chew pollen and to mould wax to build honeycomb.
- Proboscis is a temporary functional organ in honey bee. It is made temporarily by collecting parts of maxillae and labium to create a tube for drawing up liquids.
- Hypopharynx is a long flat needle like stylet. It forms food channel with labrum-epipharynx for sucking blood. It also has salivary duct that discharges saliva into blood of warm blooded animals.
- Haustellum is a middle part of the proboscis and has a median groove on its dorsal side. The hypopharynx with salivary canal and labrum-epipharynx are enclosed in the groove.
- Salivary gland in cockroach is situated in thorax on either of dorso lateral sides of esophagus. It is a pair of bipartite, diffuse and whitish in colour. Each gland has many secreting lobules or acini in grape like clusters joined together with thin tubules.
- Digestion is the chemical transformation of large and complex molecules in food to smaller molecules that can be absorbed through gut wall for insect nutrition.

NOTES

- As exoskeleton is impermeable in terrestrial insects respiratory gases move into insect body via a series of internal tubes known as tracheae or tracheal tubes.
- The tracheae are larger tubes of tracheal system, running inward from spiracles and divided into finer branches, smallest branch of which are about 2 mm in diameter.
- Abdominal muscles also called tergosternal muscles of cockroach have alternate contraction and relaxation results in rhythmic contraction and expansions of abdomen.
- Many aquatic insects get air straight from surface through hollow breathing tubes also called **siphons.**
- Air bubbles are temporary air stores or gas stores (**compressible or physical gills**) which are common means of storing and extracting oxygen by some aquatic insects.
- The thin film of air maintained on body surface which is connected with tracheal system through spiracles is called as plastron.
- Haemolymph fills haemocoel and circulates around body, bathing the tissues directly. It contains fluid plasma in which nucleated cells, called as haemocytes, are suspended.
- Haemolymph is generally colourless but is sometimes yellow or green. Some midges have hemoglobin in their blood and so heamolymph looks red.
- Prohemocytes are small, spherical or ellipsoidal cells whose nucleus occupy almost all cytoplasm.
- Plasmatocytes or phagocytes are cells of variable shape and size, with a centrally placed, spherical nucleus surrounded by more vacuolated cytoplasm.
- Granulocytes are round or disc like in shape, with a small nucleus enclosed by cytoplasm filled with prominent granules.
- Oenocytoids are spherical or ovoid cells having one or two, small and eccentric nuclei.
- Spherule cells are easily identifiable cells whose central nucleus is normally covered by mass of dense spherical inclusions occupying most of cytoplasm.
- Cystocytes or coagulocytes are spherical cells in whose small central nucleus.
- Posterior part of vessel is called as heart and has valves known as ostia. While cephalothoracic that is anterior part of vessel and a simple tube known as aorta.
- The spaces or chambers enclosed by diaphragms are known as sinuses.
- Insect heartbeat involves contraction of heart (systole) followed by a phase of relaxation (diastole) and sometime a third phase diastasis follow diastole.
- Systole is contraction phase of heartbeat, caused by contractions of intrinsic muscles of heart wall.

- Diastole is expansion phase when haemolymph enters heart caused by relaxation of heart muscles.
- Elimination of waste products of metabolism, mainly nitrogenous compounds from insect body is called as excretion.
- The process of excretion helps insect to maintain salt water balance and thus physiological homeostasis.
- The process of excretion occurs through hindgut having Malpighian tubules, ileum and rectum.
- A fluid is produced in Malpighian tubules to carry excreted materials to hindgut. This fluid is known as primary urine.
- Isotonic refers to a solution having same solute concentration as in a cell or a body fluid.
- Hypertonic solution with a higher solute concentration than that in another solution.
- Freshwater insects can regulate their haemolymph osmotic pressure successfully to point at which external environment becomes isosmotic with haemolymph. This is achieved by production of urine that is hypoosmotic to haemolymph.
- Cells that absorb ions from, or secrete them into surrounding medium are called as chloride cells. But they also transport other ions in addition to chloride. They have deeply folded plasma membrane, either at apical or basal surface and abundant mitochondria.

1.10 KEY TERMS

- **Integument**: The outermost layer of insect's body is called as integument or body wall.
- **Epidermis**: Epidermis is an inner unicellular layer below endocuticle and lying on basement membrane.
- **Cuticle**: Cuticle is outermost thick layer of integument and is mainly produced from the cells of epidermis.
- **Procuticle**: A thick inner layer of cuticle is called the procuticle. It is made up of mainly chitin, proteins and other compounds.
- **Epicuticle:** Epicuticle is a thin outermost layer of cuticle and varies in thickness from 1-4μ. It provides the property of impermeability to entire cuticle.
- **Cuticulin layer:** Cuticulin layer is an amber colour thin layer above epidermis and supported by outer polyphenol layer.
- **Arthropodin:** Arthropodin is soft, untanned and water soluble protein found in endocuticle.
- **Sclerotin:** Sclerotin is amber coloured tanned cuticular protein and found only in exocuticle.

- **Resilin:** Resilin is a colourless elastic cuticular protein provides flexibility to sclerites.
- **Apolysis:** The dissolution of old cuticle and formation of new cuticle is known as apolysis.
- **Ecdysis:** The process of the actual shedding of the old cuticle is called as ecdysis.
- **Suture:** Any kind of line or narrow space separating sclerotic areas of cuticle is called a suture.
- **Apodemes:** Any rigid ingrowths of integument are called apodemes.
- **Intima**: Cells of foregut and hindgut secrete cuticle. The cuticle lining of foregut and hindgut is known as intima.
- **Foregut**: Foregut or stomodeum is the anterior part of alimentary canal.
- **Esophagus:** The esophagus or oesophagus is a simple tube connecting the pharynx and crop.
- **Crop:** The crop is a storage organ is an extensible part of foregut just after the esophagus.
- **Midgut:** The midgut also called ventriculus/mesenteron/stomach is the middle section of alimentary canal.
- **Trophallaxis**: The mutual or unilateral exchange of alimentary fluid, including saliva, is called trophallaxis.
- **Digestion**: Digestion is the chemical transformation of large and complex molecules in food to smaller molecules that can be absorbed through gut wall for insect nutrition.
- **Plastron**: The thin film of air maintained on body surface which is connected with tracheal system through spiracles is called as plastron.
- **Haemocytes**: Haemocytes are cells residing in haemolymph.
- **Prohaemocyte**: Prohemocytes or stem cells are small, i.e., 10 μm or less in diameter, spherical or ellipsoidal cells whose nucleus occupy almost all cytoplasm.
- **Plasmatocyte**: Plasmatocytes are cells of variable shape and size, with a centrally placed, spherical nucleus surrounded by more vacuolated cytoplasm.
- **Granulocyte**: Granulocytes are round or disc like in shape, with a small nucleus enclosed by cytoplasm filled with prominent granules.
- **Oenocytoid:** Oenocytoids are spherical or ovoid cells having one or two, small and eccentric nuclei.
- **Cystocytes:** Cystocytes or coagulocytes are spherical cells in whose small central nucleus.
- **Endocytosis:** It is a process through which a cell plasma membrane folds around any foreign or insect's own substance.
- **Haemocoel**: Haemocoel is the body cavity of insects where heamolymph flows.

- **Sinuses:** The spaces or chambers enclosed by diaphragms are known as sinuses.
- **Systole:** Systole is contraction phase of heartbeat, caused by contractions of intrinsic muscles of heart wall.
- **Diastole:** Diastole is expansion phase when haemolymph enters heart caused by relaxation of heart muscles.
- **Excretion**: Elimination of waste products of metabolism, mainly nitrogenous compounds from insect body is called as excretion.
- **Primary urine:** A fluid is produced in Malpighian tubules to carry excreted materials to hindgut is known as primary urine.
- **Osmosis:** Osmosis is movement of solvent molecules through a semipermeable membrane from a region having low solute concentration to a region having high solute concentration.
- **Osmotic pressure:** Osmotic pressure is the minimum pressure that must be applied to a solution to halt the flow of solvent molecules through a semipermeable membrane.
- **Isotonic:** Isotonic refers to a solution having same solute concentration as in a cell or a body fluid.
- **Hypertonic:** Solution with a higher solute concentration than that in another solution.
- **Hypotonic:** A solution that contains fewer dissolved particles than that in normal cells and blood.
- **Active transport:** Active transport is type of cellular transport in which materials are transported across a biological membrane towards the region that already has a lot of these materials.
- **Diffusion:** Diffusion is movement of a molecule down a concentration gradient that is from an area of its high concentration to an area of its low concentration.
- **Chloride cells**: Cells that absorb ions from or secrete them into surrounding medium are called as chloride cells.

1.11 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. What is the structure of insect integument?
2. What is peritrophic membrane?
3. Differentiate between endocuticle and exocuticle.
4. Write a short note on types of epicuticle layers.
5. Draw the chemical structure of chitin.
6. What are chemical compositions of cuticle?

7. Write a brief note on integument of cockroach.
8. Distinguish between molting and sclerotization.
9. Write a brief note on structure of alimentary canal of insect.
10. What are the biting and chewing mouthparts of cockroach?
11. Define the following terms:
    i. Tracheoles
    ii. Haemocytes
    iii. Transcellular pathway
    iv. Active transport
12. What are the respiratory organs in terrestrial insects?
13. Write the summary of respiration process.
14. Distinguish between closed and open tracheal system.
15. Give a brief note on structure and function of haemolymph.
16. Write about any three types of haemocytes.
17. Why siphons are important?
18. What are sinuses and diaphragms?
19. Write functions of Malpighian tubules.

Long-Answer Question

1. Explain the structure, function and modifications of insect integuments.
2. Draw a well labelled diagram to show insect integument with labeled diagram.
3. Elaborate a note on moulting and sclerotization.
4. Illustrate schematic representation of moulting process with the help of chart.
5. Discuss about the alimentary canal in different types of insects.
6. Explain with the help of well labelled diagram the longitudinal section of crop and gizzard and transverse section of gizzard in cockroach.
7. Explain the structure and modifications of alimentary canal in insects.
8. Write a descriptive note on food, feeding and digestion in insects.
9. Explain the nutritional requirements of insects.
10. Describe the structure and physiology of respiratory organs in terrestrial insects, aquatic insects and parasitic insects.
11. Discuss in detail about haemolymph and its functions.
12. Elaborate a note on circulatory organs and mode of circulation in insects.
13. Discuss in detail about the excretory organs and physiology of excretion in insect.
14. Explain how salt and water regulation is conducted in insects.

1.12 FURTHER READINGS

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NOTES

UNIT 2 NEUROENDOCRINE, NERVOUS, SENSORY AND MUSCULAR SYSTEMS

Structure

2.0 INTRODUCTION

The neuroendocrine system plays central roles in regulation of different physiological and behavioral processes of insects. An insect's nervous system is a network of specialized cells called neurons that serve as an 'information highway' within the body. These cells generate electrical impulses that travel as waves of depolarization along the cell's membrane. Every neuron has a nerve cell body where, the nucleus is found and filament-like processes, i.e., dendrites, axons, or collaterals that propagate the action potential. Signal transmission is always unidirectional, i.e., moving toward the nerve cell body along a dendrite or a collateral and away from the nerve cell body along an axon.

Neurons are usually divided into three categories, depending on their function within the nervous system: Afferent (sensory) neurons, i.e., these bipolar or multipolar cells have dendrites that are associated with sense organs or receptors. They always carry information toward the central nervous system. Efferent (motor) neurons, i.e., unipolar cells that conduct signals away from the central nervous system and stimulate responses in muscles and glands. Internuncial (association) neurons, i.e., unipolar cells often with several collaterals and/or branching axons that conduct signals within the central nervous system.

Individual nerve cells connect with one another through special junctions, called synapses. When a nerve impulse reaches the synapse, it releases a chemical messenger (neurotransmitter substance) that diffuses across the synapse and triggers a new impulse in the dendrite(s) of one or more connecting neurons. Acetylcholine, 5-hydroxytryptamine, dopamine, and noradrenaline are examples of neurotransmitters found in both vertebrate and invertebrate nervous systems. Nerve cells are typically found grouped in bundles. A nerve is simply a bundle of dendrites or axons that serve the same part of the body. A ganglion is a dense cluster of interconnected neurons that process sensory information or control motor outputs.

The insect sensory systems are crucial for their success. The major modes of the sensory systems include vision, mechanoreceptors and audition, gustatory and olfactory chemosensory. Insects perceive light by a number of different receptors called photoreceptors. Photoreceptors found in insects are compound eyes, ocelli and stemmata. Insects can produce sounds that spread through air or water and vibrations transmitted through substrate on which they are resting.

Mechanoreceptors are important in insects to sense about environment, such as sensing vibrational signals (hearing), temperature and moist, etc. Generally, sense of taste involves direct contact with a substrate known as gustatory chemoreception. Olfaction or smell involves detection of chemicals in gaseous or airborne form termed as olfactory chemoreception. Therefore, insects use various sense organs to perceive their environment and send mechanical signals to communicate with other insects.

Muscles control all the external and internal movements of insects. All insect muscles are striated, like vertebrate muscle. Unlike vertebrates, they do not have smooth (non-striated) muscles. In their structure, protein content, contractility and regulation, insect muscles display high levels of homology to vertebrate muscles. Variations of movements and modes of locomotion in insects have resulted in a different variety of muscle having specializations in structure, function and regulation.

In this unit, you will study about neuroendocrine secretion in insects and its function, general plan of nervous system in insects, structure and functions of various visual organs in insects, physiology of vision, sound producing organs and mechanism of sound production, types of songs and their significance, physiology of various types of mechanoreceptors and chemoreceptors and structure of various types of muscles in insects and its physiology.

2.1 OBJECTIVES

After going through this unit, you will be able to:

- Explain neuroendocrine secretion in insects and its function

- Discuss the main components of nervous system
- Understand the structure and functions of various visual organs in insects
- Analyse the physiology of vision
- Explain how and why insects produce sound and songs
- Discuss about the various types of mechanoreceptors and chemoreceptors
- Describe the structure and types of muscles in insects

NOTES

2.2 NEUROENDOCRINE SECRETION IN INSECTS AND ITS FUNCTION

Regulation and synchronization of insect development is controlled by neuroendocrine system. The neuroendocrine system comprises of nervous system and endocrine glands. The most important part of the system is neurosecretory cells located in central nervous system. They are responsible for transmission of neural messages to the endocrine glands or other tissues. Neuroendocrine system has direct effects of their secretions on target in individual.

The endocrine organs produce hormones that travel in blood or heamolymph to different organs of body, coordinating their longer term activities. There are two kinds of endocrine organs in insects: i. specialized endocrine glands; and ii. neurosecretory cells, most of which are within the central nervous system.

2.2.1 Endocrine Glands

Endocrine glands are ductless glands or secretory organs of endocrine system that secrete their products, hormones, directly into circulatory system. There are various endocrine glands having different secretions and functions in insects. Secretions and functions of various glands are followed as:

i. Prothoracic Glands

Prothoracic or ecdysial glands are a pair of diffuse glands at back of head or in thorax (Refer Figure 2.1). But in silverfish, prothoracic glands are present at base of labium. These glands comprise of irregular masses of tissues having ectodermal origin and are typically closely connected with tra-cheae. These glands can or cannot be supplied with nerves. Based upon its final location, these glands are also recognized to be as thoracic or peritra-cheal or ventral glands or tentorial glands.

Secretions and Functions

The prothoracic gland is stimulated by brain hormone to produce another hormone known as **moulting hormone**. Moulting hormones are ecdysteroids produced in immature insects (larvae or nymphs). In most insects, the main ecdysteroid released is ecdysone. Ecdysone is then transported by haemolymph to specialized cells in the epidermis known as **moulting fluid cells**. These cells are stimulated by ecdysone to produce moulting fluid. Moulting fluid contains enzymes which digest away a portion of old cuticle and aid insect in moulting process. The cells of these glands exhibit cyclic secretory activity, reaching to a maximum between moults. The glands degenerate in adult insects.

Adult females produce same hormones to regulate embryonic development. The follicle cells in the ovary of adult females are principal source. Ecdysteroids are also produced in testes of some male insects, where they regulate development of male tract.

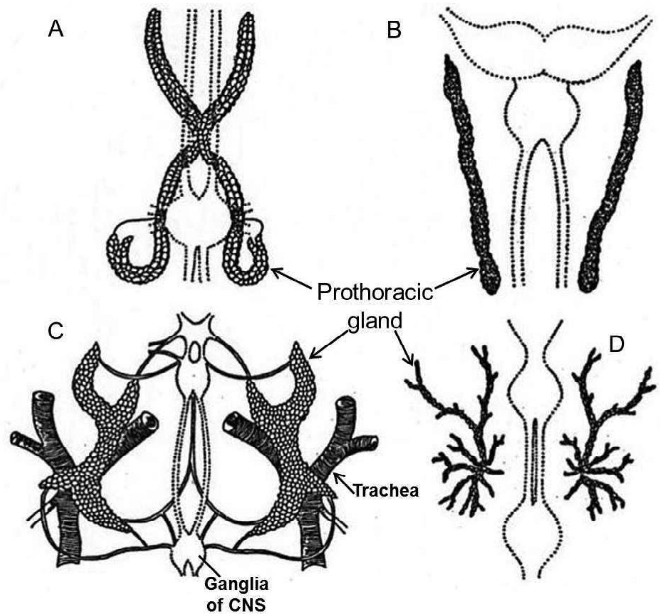

Fig. 2.1 *Prothoracic Glands in A. Cockroach, B. Bug, C. Butterfly; and D Bee*

ii. Corpora Allata (CA)

The corpora allata (singular corpus allatum) are paired glandular forms, situated one on each side of esophagus (Refer Figure 2.2). The corpora allata arise from lateral ventral ectoderm in the head adjacent the root of mandibles and maxillae. These small cellular bodies move dorsally and centrally and come to rest just behind the brain in different locations, usually ventral position, based on the insect order. In highly advanced insect orders, the glands are more dorsal and placed on upper of the esophagus below the dorsal vessel.

Each glandular body of paired corpora allata is joined with the corpus cardiacum on the same side through a nerve carrying fibers from neurosecretory cells of the brain. Also, a fine nerve links each lobe of corpus allatum with the sub-esophageal ganglion.

Secretions of Corpora Allata (CA)

Corpora Allata (CA) synthesize one of most essential hormones for insect development known as Juvenile Hormone (JH). Corpora allata, through mevalonate pathway, synthesize juvenile hormone which is an acyclic lipophilic sesquiterpene. There are number of types with slightly different structures namely JH0, I, II and III having 19, 18, 17 and 16 carbon atoms, respectively. JHIII is found in majority of the insects while JHI and II are found chiefly in butterflies, and JH0 only found in eggs of butterflies and moths.

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Functions of Corpora Allata (CA)

The Juvenile Hormone (JH), like ecdysteroids, has many functions. As its name suggests, this hormone has a main role in morphogenesis and to regulate metamorphosis of hemimetabolous (incomplete metamorphosis) and holometabolous (complete metamorphosis) insects. Presence of JH maintains the immature stages of insects and its absence permits development of adult through process of metamorphosis. In many insects, juvenile hormone also controls reproductive functions. For example, it has role in adult female of some insects for production and accumulation of yolk in oocytes.

iii. Corpora Cardiaca (CC)

The Corpora Cardiaca (CC) (singular corpus cardiacum) are a paired organ or single structure. It is placed posterior to brain and attached with aorta (Refer Figure 2.2). In higher insect orders, for example Lepidoptera (butterflies and moths), Coleoptera (beetles) and certain Diptera (flies), they are separated from aorta. In adult Hornworm, corpora cardiaca is fused with corpora allata. Corpora cardiaca is absent in Collembola (springtails).

The corpora cardiaca have axon terminals arising from both lateral Neurosecretory Cells (lNSC) and medial Neurosecretory Cells (mNSC) of brain. These are extrinsic as the neurosecretory cell bodies situated in a different place. Also, they have intrinsic neurosecretory cells that possess both their cell bodies and axons placed completely within corpus cardiacum.

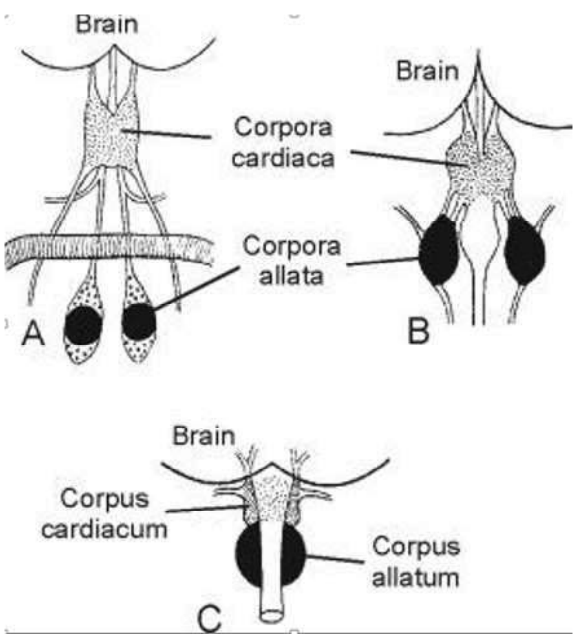

Fig. 2.2 *Location and Structure of Corpus Allatum and Corpus Cardiacum in; A. Mosquito, B. Cockroach; and C. Bug*

Secretions of Corpora Cardiaca (CC)

The Corpora Cardiaca (CC) serve as main neurohemal organ in insects and secretes several types of neuropeptides or hormones. The most important neurohormones stored and secreted by corpora cardiaca is Prothoracicotropic Hormone (PTTH), earlier known as brain hormone or ecdysiotropin. PTTH is basically the product of median neurosecretory cells of brain.

CC secretes an ovarian ecdysteroidogenic hormone in mosquitoes. They also secrete adipokinetic hormone, numerous neuroparsins and myotropins, and pheromone biosynthesis activating neuropeptide in some insect groups.

Function of Corpora Cardiaca (CC)

Secretion of Prothoracicotropic Hormone (PTTH) regulates moulting process by activating prothoracic glands to synthesize moulting hormone. Majority of insects secrete PTTH from their neurohemal organ depending on environmental stimuli, such as photoperiod, temperature, and nervous stimuli. For example, in Rhodnius bugs, moulting occur after large blood ingestion that led to abdominal distention. It eventually activates stretch receptors which then pass on information to brain to secrete PTTH.

Intrinsic cells of corpora cardiaca produce hyperglycemic and Adipokinetic Hormones (AKH) which are important in carbohydrate and lipid metabolism respectively. They also produce hormones which stimulate heartbeat rate, gut peristalsis and writhing movements of Malpighian tubules.

iv. Ring Gland

The larvae of true flies (Cyclorrhapha: Diptera) have a small ring of tissue, held through tracheae, referred as the ring gland or Weismann's ring (Refer Figure 2.3). Ring glands are formed from fusion of corpus allatum, corpus cardiacum and thoracic glands. Ring glands have different cells but are homologous with corpus allatum, corpus cardiacum and thoracic glands. The ring gland adjoins the aorta exactly above brain. The ring gland is attached to brain through a pair of nerves and it also possesses a link with recurrent nerve. It secretes puparium hardening hormone and controls metamorphosis in flies.

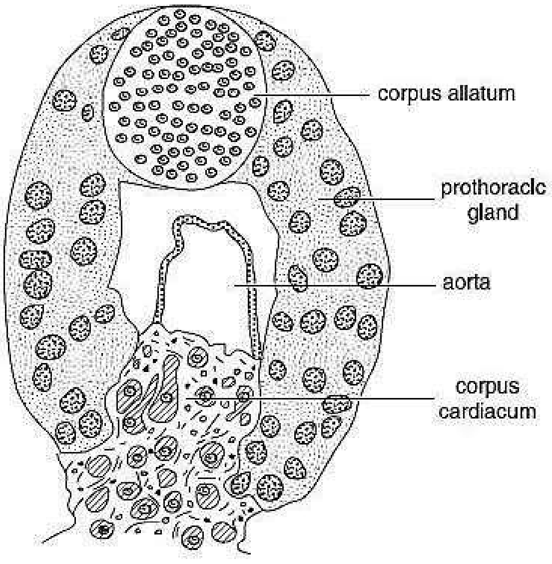

Fig. 2.3 *Ring Gland in Hover Fly*

v. Epitracheal Glands

Epitracheal glands are found in highly evolved insects such as butterflies, flies some beetles and bees. These glands contain 16–18 large neurosecretory cells bound to a trachea neighboring each spiracle. The neurosecretory cells here are also called as **Inka cells**. These cells are responsible for secretion of two hormones namely Ecdysis-Triggering Hormone (ETH) and Pre-Ecdysis-Triggering Hormone (PETH). These hormones are particularly involved with ecdysis.

vi. Midgut Endocrine Cells

The cells in midgut epithelium are supposed to be endocrine cells as these cells have such type of ultrastructure and immunocytological properties. These are isolated cells dispersed within the chief midgut cells. They rest on the basement membrane of the midgut and are, thus, directly associated with haemolymph. These cells synthesize biologically active peptides. For example, endocrine cells in midgut of mosquitoes are immunoreactive to four types of antisera, each cell having just one peptide. It regulates synthesis of digestive enzymes. Midgut endocrine cells contain diuretic hormone that stimulate ions and water transport by Malpighian tubules. Secretions of midgut endocrine cells also act in regulating gut wall motility.

2.2.2 Neurosecretory Cells

Neurosecretory cells are present in ganglia of central nervous system. They usually look like monopolar nerve cells. They typically secrete their products into haemolymph. Somata of neurosecretory cells occur in all ganglia of central nervous system.

Neurohemal Areas or Organs

The regions where products of neurosecretory cells are secreted into haemolymph are termed as neurohemal areas, or when a well-defined structure is made called as neurohemal organs. The corpus cardiacum is a neurohemal organ where various types of hormones synthesized in brain and move to haemolymph.

Variations in Neurosecretory Cells

There are two main groups of neurosecretory cells on each side of brain. One group of neurosecretory cells called median Neurosecretory Cells (mNSC) is in pars intercerebralis which is anterior midline of brain (Refer Figure 2.4). mNSC occur in two groups, one on each side of midline. Their axons pass down through brain and normally terminate in a pair of neurohemal organs, i.e., corpora cardiaca where neurosecretion is stored.

In some insects, for example housefly, some neurosecretory axons do not terminate in the corpora cardiaca but pass through them to corpora allata. In many bugs and aphids, axons bypass corpora cardiaca and instead terminate in nearby aorta wall. In aphids, some neurosecretory axons transport their product directly to target organ. The axons of mNSC which produce bursicon terminate in fused thoracic-abdominal ganglion of true flies and in last abdominal ganglion of cockroaches and locusts. The number of neurosecretory cells in this group varies with different species. For example, Locust has about 500, whereas Aphid has only four or five.

NOTES

Second group of neurosecretory cells in brain exhibit great variation in its location. It is sometimes medial to mushroom bodies (also called corpora pedunculata) and sometimes between the mushroom bodies and the optic lobes. In some flies and bees, neurosecretory cells of this group are involved with other neurosecretory cells in pars intercerebralis. A second axon tract runs from these cells through brain to corpora cardiaca and in Locust, some nerve fibers expand to corpora allata.

Also, in the protocerebrum are two groups of lateral Neurosecretory Cells (lNSC) whose axons do not cross but travel to the corpus cardiacum of the same side.

Neurosecretory cells are also found in all of the ventral ganglia. Numbers of neurosecretory cells that arise in ventral ganglia quite vary. Their products are secreted into haemolymph at several neurohemal locations. For example, the axons of cells in the sub-esophageal ganglion of tobacco hornworm pass to corpus cardiacum through brain or lateral nerves.

Secretions and Functions of Neurosecretory

Following are the secretions and functions of neurosecretory cells (Refer Table 2.1 and Figure 2.4)

- Products of mNSC are as follows:
  - o Prothoracicotropic Hormone (PTTH), which activates molt glands.
  - o Allatotropic and allatostatic hormones, whose primary function is to regulate the activity of the corpora allata.
  - o Diuretic hormone, which affects osmoregulation.
  - o Ovarian Ecdysiotropic Hormone (OEH) (formerly egg development neurosecretory hormone).
  - o Ovulation- or oviposition-inducing hormone.
  - o Testis Ecdysiotropin (TE).
- Bursicon is important hormone for cuticular tanning. It is secreted from mNSC in some insects. It is principally found in abdominal ganglia and released via abdominal perivisceral organs.
- Neurosecretion from mNSC also affects behaviour. In many cases this is an indirect action and is important in protein synthesis.
- Eclosion Hormone (EH) works in ecdysis and is produced by neurosecretory cells in tritocerebrum.
- Neurosecretion from sub-esophageal ganglion is, in cockroaches, synthesized and released regularly and controls circadian rhythm of locomotor activity.
- In many female moths, Pheromone Biosynthesis Activating Neuropeptide (PBAN) is produced in neurosecretory cells in sub-esophageal ganglion. The PBAN synthesized in sub-esophageal ganglion and released via corpora cardiaca.

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- In female pupae of silk moth, neurosecretory cells in sub-esophageal ganglion produce a diapause hormone. It promotes development of eggs that enter diapause.

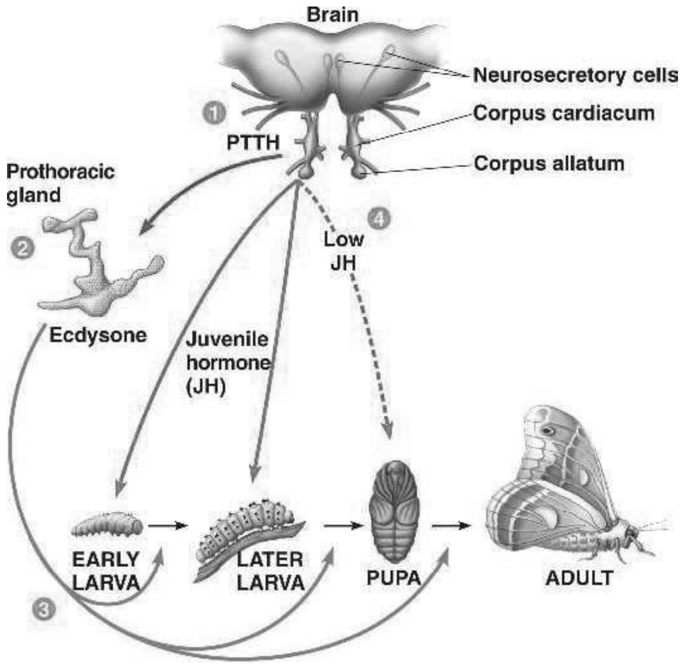

Fig. 2.4 *Role of Neuroendocrine Secretions in Moulting and Metamorphosis in Butterfly*

Insect Hormones and their Roles

Hormones are chemicals produced by an organism which circulate in blood to regulate its long term physiological, developmental and behavioural activities. Sources of hormones secretion are different from their target where they act. Hormones are non-neural and neural types. Source of secretion, target and functions of different hormones are given in Table 2.1

Table 2.1 *Hormones: Source, Target and Function in Insect*

S.No.	Hormones	Source	Target	Function
I.	**Non-Neural Hormones**			
1.	Immature Insects			
	Ecdysone	Ecdysial gland	Epidermis	Initiate moulting
	Juvenile Hormone (JH)	Corpora allata	Epidermis	Controls metamorphosis
2.	Adult Insects			
	Ovarian Hormone (Ecdysteroids)	Follicle cells in ovary	Fat body	Initiate and regulate production of vitellogenin
	Juvenile Hormone (JH)	Corpora allata	Fat body	Make fat body competent to produce vitellogenin

NOTES

II.	Neural Hormones and Peptide Hormones			
1.	Ecdysiotropin, i.e., Prothoracicotropic Hormone (PTTH)	Brain hormone protocerebrum	Ecdysial glands	Stimulate production and release of ecdysone
2.	Bursicon	mNSC and thoracic abdominal ganglion of flies	Epidermis	Stimulates sclerotization and melanization (tanning) of cuticle
3.	Eclosion Hormone	Brain of pre-ecdysis moths	Abdominal ganglion	Synchronization of eclosion with photoperiod
4.	Ecdysis-triggering Hormone	Epitracheal glands	CNS (abdominal ganglia)	Trigger a behaviour sequence critical for shedding of exocuticle at larval stages
5.	Allatostatins (Neuropeptide Hormone)	mNSC-Brain	Corpora allata	Inhibit juvenile hormone synthesis
6.	Allatotropin	Brain-mNSC	Corpora allata	Stimulate juvenile hormone synthesis
7.	Diuretic Hormones	NSC-CNS, CC	Malpighian tubules	regulate water balance or fluid secretion
8.	Proctolin	Brain/CC	Gut, Muscles	Stimulate contraction of visceral and skeletal muscles. Regulate heartbeat, defecation
9.	Ovarian Ecdysteroidogenic Hormone (OEH)	Brain	Ovaries	Stimulate ovarian tissue to produce ecdysteroids
10	Hypo + Hyperglycemic Hormones	Brain/CC	Fat body	Controls glycogen to trehalose. Maintain level of blood sugar
12	Adipokinetic Hormones (AKH)	Brain/CC	Fat body	Regulate lipid metabolism

Neuroendocrine Secretion in Different Insects

I. Cockroach

The prothoracic glands are a pair of endocrine glands located in prothorax of cockroach. Prothoracic gland is main source of ecdysteroids in larvae of cockroach. Moulting gland of Periplaneta also secretes 3-dehydroecdysone and proteins. Moulting gland of Periplaneta is regulated in different successive steps of cooperation of nervous and neuroendocrine activity. The 17th day of larval stage is characterized as head critical period, i.e., after this period the ecdysteroid secretion of gland is independent of the Prothoracicotropic Hormone (PTTH) from the brain. Corpora allata secrete Prothoracicotropic Hormone (PTTH). This PTTH goes to prothoracicotropic gland. Main peak of ecdysteroid production is regulated by prothoracicotropic neuropeptides from the brain.

NOTES

II. Honey Bee

Endocrine Glands: Endocrine glands of larva of honey bees comprises of corpora cardiaca, corpora allata and prothoracic glands.

- Corpora allata sit either side of esophagus, they are relatively large globular bodies.
- Prothoracic glands are located at sides of Ventriculus (midgut) close to first spiracle. They are connected to sub-esophageal ganglia. Their shapes are elongated tubes.

Corpora allata and prothoracic glands work antagonistically and are important during the process of moulting in larval stage. Prothoracic gland begins to degenerate during pre-pupal stage of development.

Based upon signals from brain, the corpora allata secretes juvenile hormone which suppresses initiation of moulting process. Moulting process is initiated in response to ecdysone secreted by prothoracic gland. Both are hormones and are secreted by their respective gland into haemolymph. Brain responding to nerve sensors relating to cuticle stress reduces production of juvenile hormone, ecdysone dominates causing larva to enter a moulting stage.

Juvenile Hormone (JH): Source of juvenile hormone is corpora allata. Production of juvenile hormone is initiated in response to nerve signals received from brain via, corpora cardiaca. Effect of JH is to maintain larval stage of larva, i.e., no moulting.

Moulting Hormone-Ecdysone: Source of ecdysone is prothoracic glands. It is produced in response to a hormone released by corpora cardiaca in response to neurosecretory cell activity in brain. Hormone released by corpora cardiaca is received by prothoracic gland via haemolymph. Ecdysone causes production of enzymes that initiate moulting.

Check Your Progress

1. How is regulation and synchronization of insect development controlled?
2. What are endocrine glands?
3. Name the types of endocrine glands.
4. Define the term moulting hormone.
5. What does Corpora Allata (CA) synthesizes?
6. Where are neurosecretory cells present?
7. List the products of medial Neurosecretory Cells (mNSC).

2.3 GENERAL PLAN OF NERVOUS SYSTEM IN INSECTS

NOTES

The **nervous system** is a part of animal's body that coordinates its behaviour and transmits signals between different body areas. The nervous system have two main types of specialized cells namely neurons and glial cells. Neurons transmit signals between cells and from one part of the body to another. Glial cells regulate homeostasis and provide structural and metabolic support to neurons. Some components of neurons and glia are bundled to form nerves and ganglia (Refer Figure 2.5). Nerves include only axonal component of neurons, whereas ganglia include axons, cell bodies and dendrites. Nervous system of insects is divided into different parts according to their functions and their location in body.

2.3.1 Basic Components of Nervous System

Basically main components of nervous system are **neurons** and **glial cells**. Neurons are bundled into **nerves** and **ganglia** (Refer Figure 2.5). Details of these components are explained below:

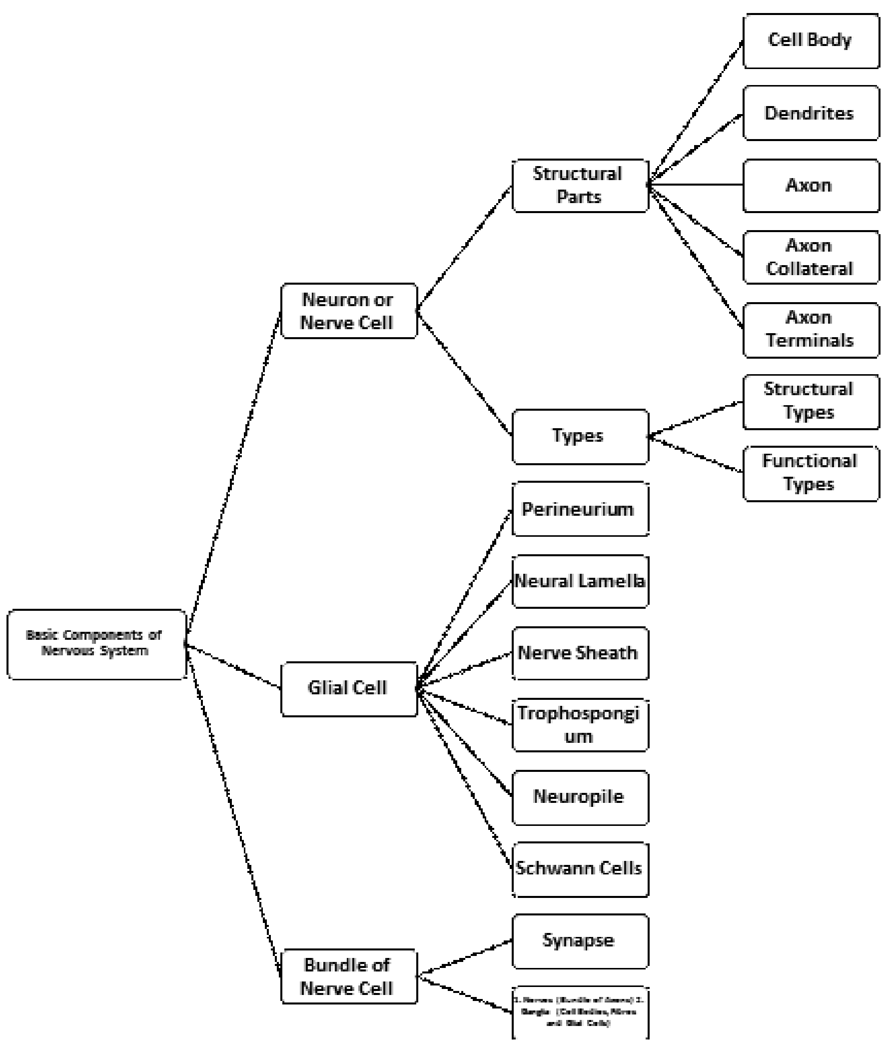

***Fig. 2.5** Basic Components of Nervous System*

I. Neurons

The basic component of nervous system is nerve cell also called as neuron. These are conducting cells responsible for transducing, conveying or processing nerve impulses.

Structure of Neuron

A neuron has a cell body with two cytoplasmic projections (nerve fibres or neurite) (Refer Figure 2.6). One projection becomes dendrite (dendron) that receives message and second form axon (neurite) that transmits information, either to another neuron or to an effector organ, such as a muscle. The detailed structure of neurons is given below:

- **Cell Body:** Cell body of neuron is called as soma or perikaryon or neurocyte. Cell body has nucleus, many mitochondria, Golgi complexes and Rough Endoplasmic Reticulum (RER). Cell body plays major role in protein synthesis.
- **Dendrites:** Dendrites are short, branched projections that extend from cell body. Dendrites receive information via several receptors situated in their membranes that bind to chemicals. These chemical messengers are known as neurotransmitters.
- **Axon**: Axon is a large projection that extends from cell body and functions to send information. As compare to shorter dendrites, an axon can extend for more than a meter. Due to its longer length, axon possesses microtubules and is enclosed by myelin. Microtubules are arranged inside the axon as parallel arrays of long strands. These microtubules act as pathways for transport of materials to and from cell body. Axon may have collateral and terminal arborization and synapse.
- **Axon Collateral:** An axon has side or lateral branches known as collaterals, so that one neuron can send information to many others. These collaterals are like roots of a tree, split into smaller extensions. Each of these extensions has a synaptic terminal on tip.
- **Axon Terminals**: When an axon reaches a target, it terminates into multiple endings known as axon terminals (terminal arborization). The axon terminal is meant to convert electrical signal into a chemical signal in a process called **synaptic transmission**. Both axon and the collateral end in terminal arborizations of fine branching fibrils.

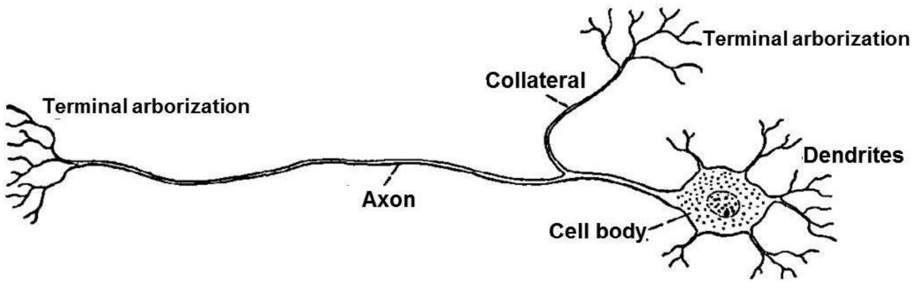

Fig.2.6 *Structure of Neuron*

Types of Neurons Based on their Structure and Function

Following is the detailed description about neurons based on their structure and function:

Structural Types of Neurons

Functional role of any neuron is dependent on its structure. There are basically three types of neurons on basis of the number of projections from cell body, namely monopolar, bipolar and multipolar neurons (Refer Figure 2.7).

- **Monopolar Neuron:** Monopolar neuron are also called unipolar neurons. These have single projection from cell body. This single projection is then splits close to cell body into two trunks, one form dendrites for incoming signals and another form an axon for outgoing signals. Central Nervous System (CNS) of almost all insect groups contains monopolar neurons.
- **Bipolar Neuron:** Bipolar neurons have two projections that extend in opposite directions from cell body. One projection form dendrite and another become axon. The peripheral sense cells are bipolar neurons having a short and generally unbranched, distal dendrite receiving stimuli from the surroundings and an adjacent axon expanding to central ganglia.
- **Multipolar Neuron:** Each multipolar neuron contains one axon and multiple dendrites. It comprises major type of neuron in human. In insects, these neurons occur in ganglia of nervous system and are also involved with stretch receptors.

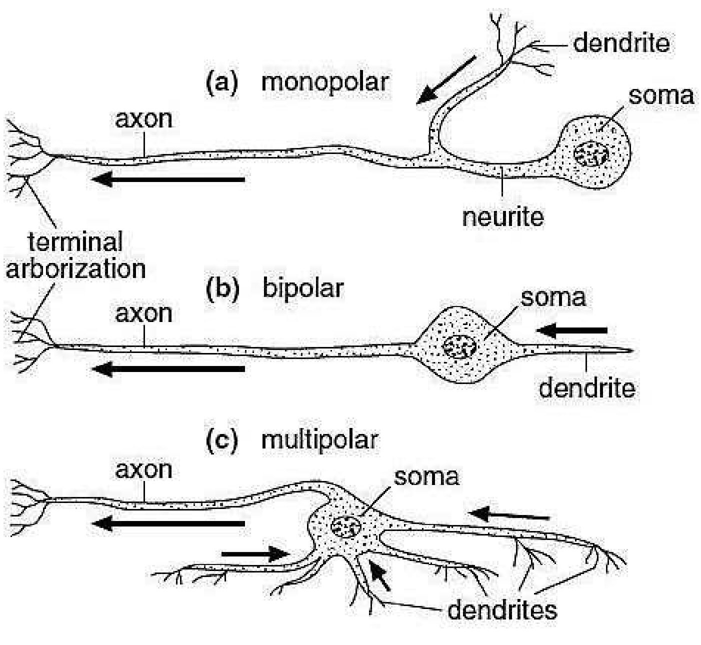

Fig. 2.7 *Types of Neuron Based on Number of Projections*

Note: Arrow Shows Direction of Conduction

Functional Types of Neurons

Neurons are functionally categorized on the basis of direction in which signal travels in relation to Central Nervous System (CNS). There are three functional types of neurons: sensory, motor and interneurons.

- **Sensory Neurons:** Sensory or afferent neurons are generally bipolar but can be multipolar neurons have dendrites that are near to sense organs or receptors. They always carry information toward central nervous system.
- **Motor Neurons:** Motor or efferent neurons are unipolar cells that carry impulses or signals from central nervous system and stimulate responses in muscles and glands. Their cell bodies are located within a ganglion.
- **Interneuron Neurons**: Interneurons (internuncial or association) neurons transmit information from sensory to motor neurons or other interneurons. These may be mono- or bipolar and their cell bodies occur in a ganglion.

Majority of the neurons in Central Nervous System (CNS) are interneurons. Interneurons are categorized into two type namely local and inter-segmental interneurons. **Local interneurons** are restricted to an individual ganglion and they can be spiking or non-spiking. **Inter-segmental interneurons** convey information along nerve cord. Fibers that carry information from anterior to posterior ganglia are known as descending fibers. Fibers that conveying information to brain or anterior ganglia are known as ascending fibers. These neurons are involved in coordinating activities of different ganglia so as to lead coordinated activity of the entire insect body.

Synapse

The terminal arborisations of an axon come very near with dendrites or axon of another neuron or they can end near a muscle, i.e., neuromuscular junction. Followings are the terms or components (Refer Figure 2.8) used in transmission of nerve impulses,

Synapse: Association between terminal arborisations and dendrites is called a synapse. Synapses are junctions where neurons receive information from or transmit it to other neurons. Impulses can be transferred across synapse either electrically or chemically.

Synaptic Cleft: Space or gap between arborisations and dendrites is called as synaptic cleft or gap.

Pre-Synaptic Terminal: Pre-synaptic terminal is a specialized area that contains neurotransmitters in synaptic vesicles. When a nerve impulse (action potential) reaches pre-synaptic terminal of sending neuron it releases small signalling molecules called neurotransmitters.

Post-Synaptic Terminal: Post-synaptic terminal is the receiving part of synapse between two neurons.

Synaptic vesicles: Synaptic vesicles are small vesicles that are clustered at presynaptic terminals. They store neurotransmitters and release them by calcium-triggered exocytosis.

Neurotransmitters: Acetylcholine is known to be main prevalent excitatory transmitter in insect nervous system. This is chief transmitter of olfactory and mechanosensory neurons and of numerous interneurons. Serotonin seems to be a co-transmitter in certain chordotonal and multipolar sensory neurons whereas histamine is transmitter in retinula cells of compound eyes and ocelli. The salivary glands of cockroaches have innervations from two kinds of neuron comprising either serotonin or dopamine.

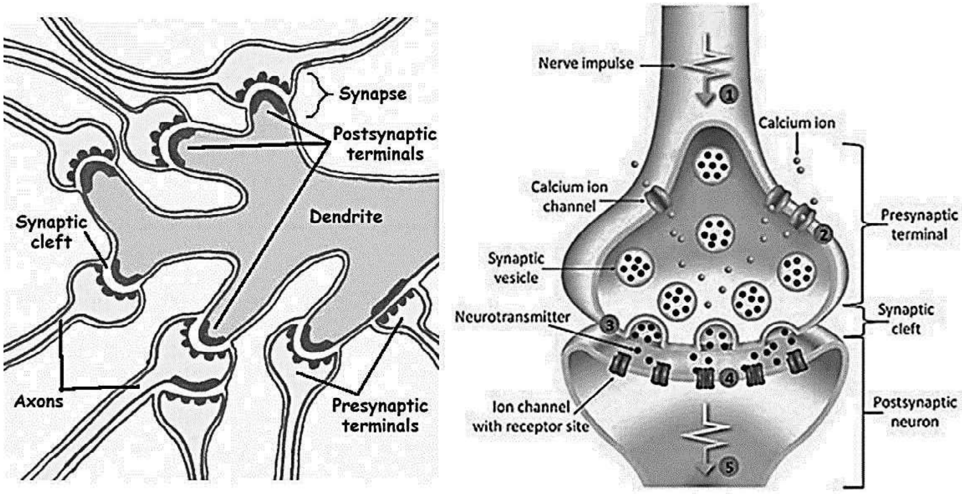

Fig. 2.8 *Components of Synapse Involved in Transmission of Nerve Impulses*

II. Glial Cells

Glial cells are non-conducting supporting cells which enclose neurons and support to protect neurons and maintain stable ionic environment. Each neuron is almost completely invaginated with folds of one or more glial cells but except for its finest branches. Synaptic contacts between neurons take place merely where glial invaginations are lacking. Glial cells (neuroglia) are present in a very large number in central nervous system. Glial cells are differentiated according to their position and function, i.e., as follows (Refer Figure 2.9):

- **Perineurium**: The peripheral glial (perineural) cells form perineurium. These are very closely associated by tight junctions, forming blood-brain barrier. This barrier is essential in isolating nervous system from haemolymph whose composition is both highly variable and unsuitable for neuronal function.
- **Neural Lamella:** Perineurium secretes a thick basement membrane on its outer side called as neural lamella. Neural lamella is a protective sheath and contains collagen fibrils and mucopolysaccharide. The lamella is freely permeable, enabling perineural cells to accumulate nutrients from haemolymph. It facilitates mechanical support for central nervous system. It holds cells and axons together thus allowing flexibility essential for movements of insect.
- **Nerve Sheath:** The perineurium and neural lamella are collectively known as the nerve sheath.
- **Trophospongium:** Inner glial cells occur around soma (perikarya or cell body) into which they extend finger-like extensions of their cytoplasm. These glial cells are called as trophospongium. The function of these cells is to transport nutrients from perineural cells to soma. Nutrients from soma are transported to their site of use by cytoplasmic streaming.
- **Neuropile:** Neuropile is a central region consisting of intermingling, synapsing axons encapsulated by processes of glial cells, called as neuropile.

- **Schwann Cells:** Wrapped around each axon or groups of smaller axons are other glial (Schwann) cells also called neurilemma. These cells isolate axons from haemolymph in which they are bathed. Unlike in vertebrates, glial cells are not compacted to form a myelin sheath but rather are loosely wrapped around axons.

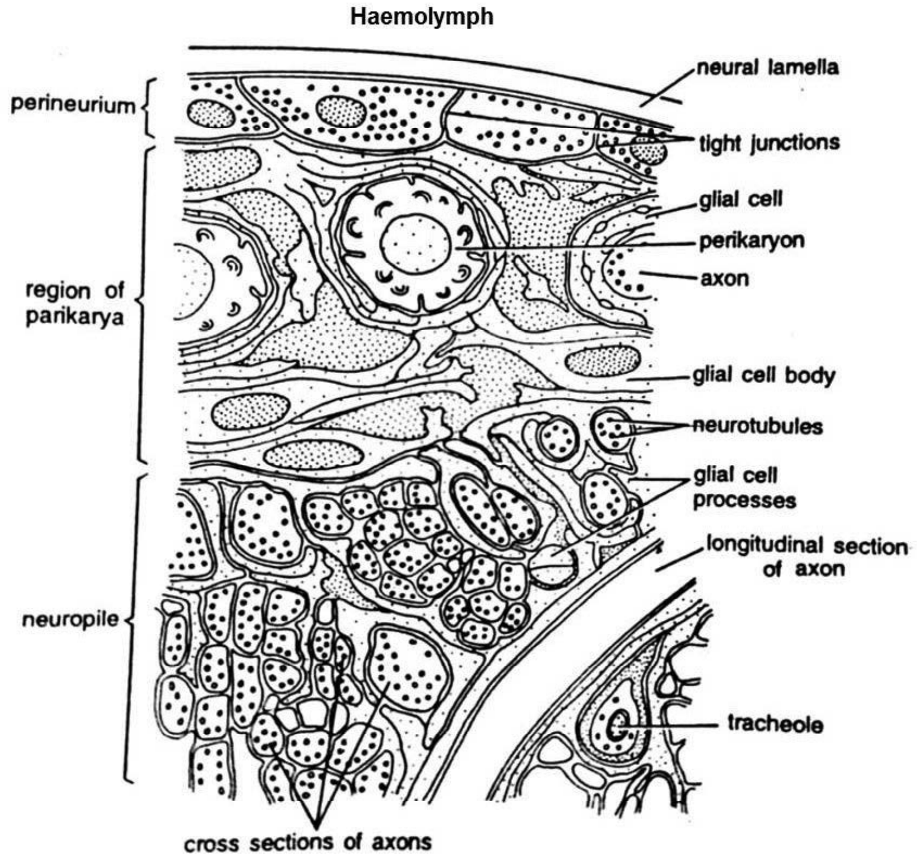

Fig.2.9 *Cross Section of Caudal Ganglion of Cockroach*

Note: Darkly shaded areas indicate extracellular spaces.

III. Nerves

Nerve cells are found grouped in bundles. Axons are primary transmission lines of nervous system and as bundles they form nerves. Thus, a nerve is a bundle of dendrites or axons that serve same part of body.

IV. Ganglia

The cell bodies of interneurons and motor neurons are grouped, with fibres (axons and dendrites) interconnecting all types of nerve cells to form nerve centers are known as ganglia. Simply a collection of cell bodies constitutes a ganglion. A ganglion processes sensory information or control motor outputs.

Ganglion cells are mostly situated at periphery of ganglion. The central part of ganglion is occupied by a dense mass of nerve fibrils, called neuropile. In addition to nerve cells, a ganglion contains glial cells which form a supporting tissue. These glial cells are generally profusely branched among elements of nerve tissue. The ganglion is surrounded by a nucleated neurilemma continuous with that of nerves

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(Refer Figure 2.10). Commissure is a transverse tract of nerve fibers connecting two ganglia of a segment. Connective is a longitudinal cord of nerve fibers connecting successive ganglia. Connectives have no cell bodies.

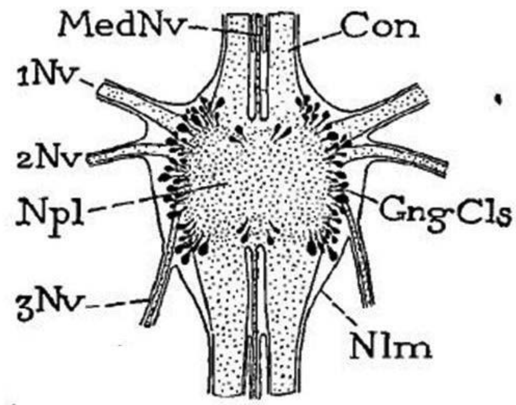

Fig.2.10 *T.S. of Abdominal Ganglion of Ventral Nerve Cord in Hawker Dragonfly*

In above Figure 2.10 following abbreviations are used which refer as: Npl-Neuropile, Gngcls-Ganglion Cells, MedNv- Median Nerve, lNv, 2Nv, 3Nv-Lateral Nerves, Nlm-neurilemma, Con-connectives.

2.3.2 Division of Nervous System

Anatomically Nervous System of insects is divided into three parts, i.e., as follows (Refer Figure 2.11):

- Central Nervous System
- Visceral Nervous System
- Peripheral Sensory Nervous System

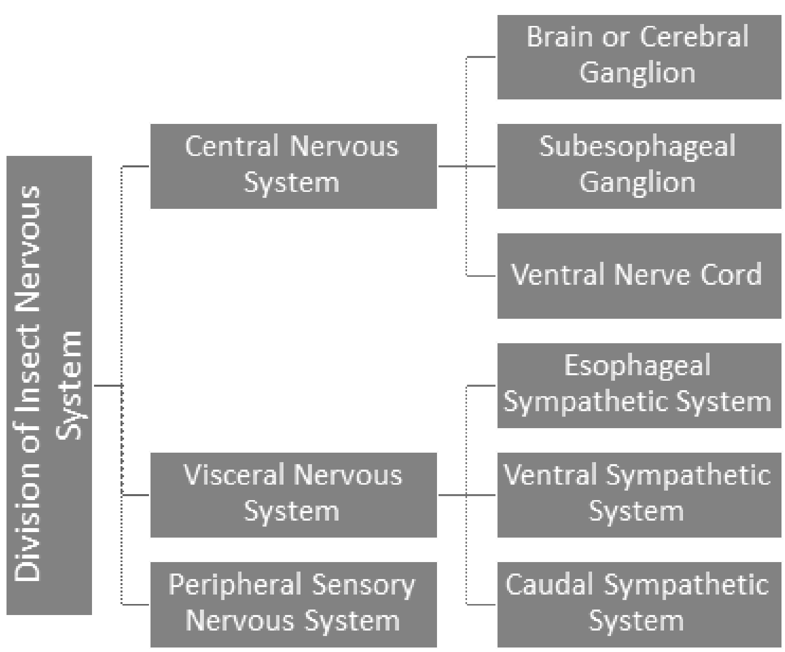

Fig. 2.11 *Division of Insect Nervous System*

I. Central Nervous System (CNS)

The Central Nervous System (CNS) is main part of nervous system. It consists of a series of ganglia which are joined together by longitudinal (connectives) and transverse (commissure) cords of nerve fibres. Usually, each segment of insect body has a pair of ganglia (Refer Figure 2.16). Generally, the two ganglia of each thoracic and abdominal segment are fused into a single structure. The ganglia of all head segments are united to form two ganglionic centers namely brain and sub-esophageal ganglion**.** Chain of thoracic and abdominal ganglia found on floor of body cavity is called as ventral nerve cord. Thus, in adult insects, central nervous system has three parts, they are as follows:

- Brain or Cerebral Ganglion
- Subesophageal Ganglion
- Ventral Nerve Cord

1. Brain or Cerebral Ganglion

The brain of an insect positioned just above esophagus and thus also called supra-esophageal ganglion. The brain is connected behind to suboesophageal ganglion by circumesophageal connectives ventral to esophagus. This is complex of six fused ganglia, i.e., three pairs of ganglia located dorsally within head capsule (Refer Figure 2.16). The brain is major interacting organ of body. It receives sensory input from sensory parts of head and through ascending interneurons, from more posterior ganglia. Brain consists of three distinct lobes from dorsal to ventral, given, as follows: Protocerebrum, Deutocerebrum and Tritocerebrum.

i. **Protocerebrum:** The protocerebrum is largest and complex part of brain and bi-lobed in appearance. It contains both neural and endocrine (neurosecretory) elements. It has united ganglia of optic segment and thus innervates (supply nerves) compound eyes and ocelli. Followings are the parts of protocerebrum:

   - **Pars Intercerebralis**: Protocerebrum has pars intercerebralis at anterodorsal region. The pars intercerebralis is a group of cell bodies present on either side of midline of brain. Anterior cells of pars intercerebralis provide fibers to nerves of ocelli.
   - **Pons Cerebralis:** Fibers from lateral cells of pars intercerebralis pass into protocerebral bridge or pons cerebralis. Pons cerebralis is a mass of neuropile located medially dorsal to central body and joining with many other parts of brain.
   - **Corpora Pendunculata:** Within protocerebrum, there is a pair of corpora pendunculata also called mushroom bodies due to their shape.

Structure of Mushroom Bodies: It is a paired structure and positioned at sides of pars intercerebralis. It has cap of neuropile called **calyx**, from where a stalk called **peduncle** extends. Peduncle splits into two or sometimes three lobes, named as α, β and γ lobes. Honey bee and Cockroach have double calyces that contain three concentric rings of neuropiles called as lip, collar and basal ring.

Mushroom bodies have large number of interneurons known as **Kenyon cells** that contain their cell bodies above calyx. Kenyon cell contains dendrites in the calyx and an axon moves down peduncle (Refer Figure 2.12B).

Importance of Mushroom Bodies: Mushroom bodies are important association centers. They receive sensory inputs, especially olfactory and visual and convey information to other protocerebral centers. Also they play a central role in learning and memory. Size of mushroom bodies varies broadly with development of complex behaviour patterns and diet patterns. They are most highly developed in social insects. For example, in worker ants, they make up about one-fifth volume of brain. Gregarious locusts have broad range of diets and more complex social communications. Therefore, these locusts have bigger mushroom bodies than that of locusts in solitary phase.

Central Complex: It is a series of four interconnected neuropiles which occupy midline of protocerebrum (Refer Figure 2.12B). From dorsal to ventral these are as follows: protocerebral bridge, fan-shaped body (upper division of central body), ellipsoid body (lower division of central body); and a pair of noduli at base. Most cells of central body contain neuropeptides that are used as neurotransmitters.

Optic Lobe: The optic lobes are lateral extensions of protocerebrum to compound eyes. Each contains three successive neuropiles called as lamina, medulla and lobula complex. Pattern of neural signals, via, these three optic neuropiles, precisely produces any image falling on eye. Fibers cross over horizontally between these neuropiles and form outer and inner optic chiasmata (Refer Figure 2.12B). Through these chiasmata the neural map of visual image is reversed along antero-posterior axis and then re-reversed.

ii. **Deutocerebrum:** Deutocerebrum is fused ganglia of antennary segment (Refer Figure 2.12 and 2.13). Deutocerebrum consists of antennal (with olfactory function) lobes and antennal mechanosensory and motor center. The antennal lobes are area of neuropile, one in relative to each antenna, within which there are separate balls of dense synaptic neuropile known as glomeruli. The number of glomeruli exhibit great variation among insect species. For example, cockroach and hornworm contain about 125 and 64 glomeruli respectively, whereas mosquito possess less than ten glomeruli. Axons arise from olfactory sensilla of antenna end in glomeruli. Axons from olfactory receptors on maxillary and labial pulps also end in glomeruli adjoining to those that receive inputs from antennae.

iii. **Tritocerebrum:** It is ganglia of third or intercalary segment of head (Refer Figure 2.12 and 2.13). It consists of two small broadly separated lobes connected to dorsal lobes of deutocerebrum. It innervates labrum and anterior region of gut. Thus, tritocerebrum is a small region of brain and consist of a pair of lobes below deutocerebrum. Circumesophageal connectives from tritocerebrum move to sub-esophageal ganglion. Tritocerebral lobes of either side are joined through a commissure running backside of esophagus. On anterior side, nerves having sensory and motor components join with frontal ganglion and labrum.

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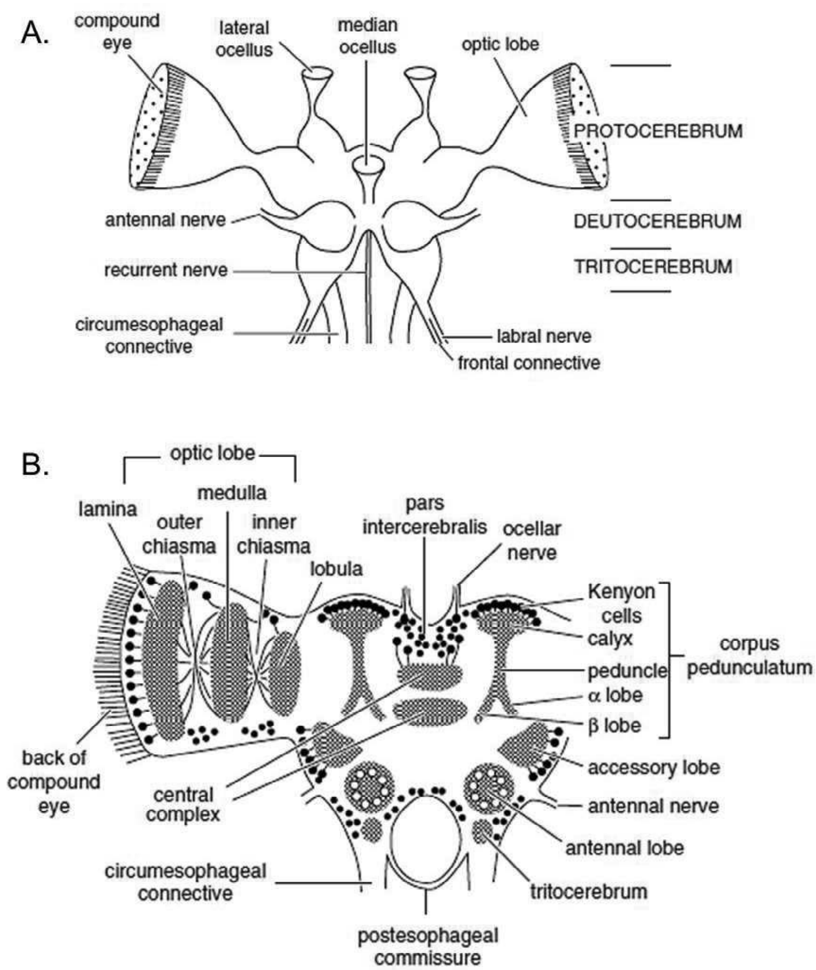

Fig. 2.12 *Brain of Locust; A. Parts of Brain and its Innervation, B. Detailed Parts of Protocerebrum with their Neuropile (Shaded)*

Note: The distribution of cell bodies is indicated by black dots.

2. Subesophageal Ganglion

It is ventral ganglionic center of head and is formed by fusion of ganglia of mandibular, maxillary and labial segments (Refer Figure 2.13). It has paired nerves that supply their corresponding appendages. It is united by a pair of stout oesophageal connectives.

From this ganglion, nerves containing both sensory and motor axons run to the mouthparts, salivary glands and neck. The ganglion is also the center for maintaining locomotor activity.

3. Ventral Nerve Cord

It is a series of ganglia aligned on floor of thoracic and abdominal region. They are combined into a longitudinal chain via support of a pair of connectives that runs from posterior margin of sub-esophageal ganglion. The first three ganglia are located one in each of segments of thorax and are called as thoracic ganglia. Rest of ganglia situated in abdomen is called as abdominal ganglia.

Thoracic Ganglia: Thoracic ganglia control the organs of locomotion. Each of thoracic ganglia has two pairs of principal nerves, one pair of which provides the common musculature of its segment and the other pair innervates the muscles of the legs. An additional pair of nerves occurs in each of the mesothoracic and metathoracic regions which control movements of wings.

Abdominal Ganglia: Each abdominal ganglion has a pair of principal nerves that supply to the muscles of its segment. The abdominal ganglia are variable in number. In primitive insects, such as jumping bristletails there are three separate pairs in thorax and eight in abdomen, last abdominal ganglion is composite. In higher insects the fusion of ganglia is more extensive. The abdominal ganglia are fewer and first abdominal pair fuses with that of metathorax. In higher flies, thoracic ganglia unite into one. In bugs, all thoracic and abdominal ganglia have combined to form a single mass.

II. Visceral (or Sympathetic) Nervous System

The visceral or sympathetic nervous system is categorized into the following:

- Esophageal Sympathetic System
- Ventral Sympathetic System
- Caudal Sympathetic System

i. Esophageal Sympathetic (Stomatogastric or Stomodeal) System

Esophageal Sympathetic system is directly associated with the brain and innervates foregut, midgut, heart and some other parts of insect. It is dorsal in position, lying above and at the side of foregut. Generally, it includes frontal ganglion, recurrent nerve which lies mediodorsally above gut, hypocerebral ganglion. It has a pair of inner esophageal nerves and a pair of outer esophageal (gastric) nerves, each of which normally terminates in an ingluvial (ventricular) ganglion situated alongside posterior foregut (Refer Figure 2.13).

Nerves within stomatogastric system both collect mechanosensory and chemical information from, and regulate muscular activity of organs they supply. In frontal ganglion, neuropile has a central pattern generator that controls rhythmic motor activity of foregut.

ii. Ventral Sympathetic System

Ventral sympathetic system consists of a pair of transverse nerves involved with each ganglion of ventral nerve cord, and each pair is connected with ganglion preceding it by a median longitudinal nerve. The transverse nerves move to spiracles on each side and dilate into one or more small ganglionic enlargements.

iii. Caudal Sympathetic System

Caudal sympathetic system includes nerves from composite terminal abdominal ganglion. This system supply nerves (innervates) to hindgut and reproductive (sexual) organs.

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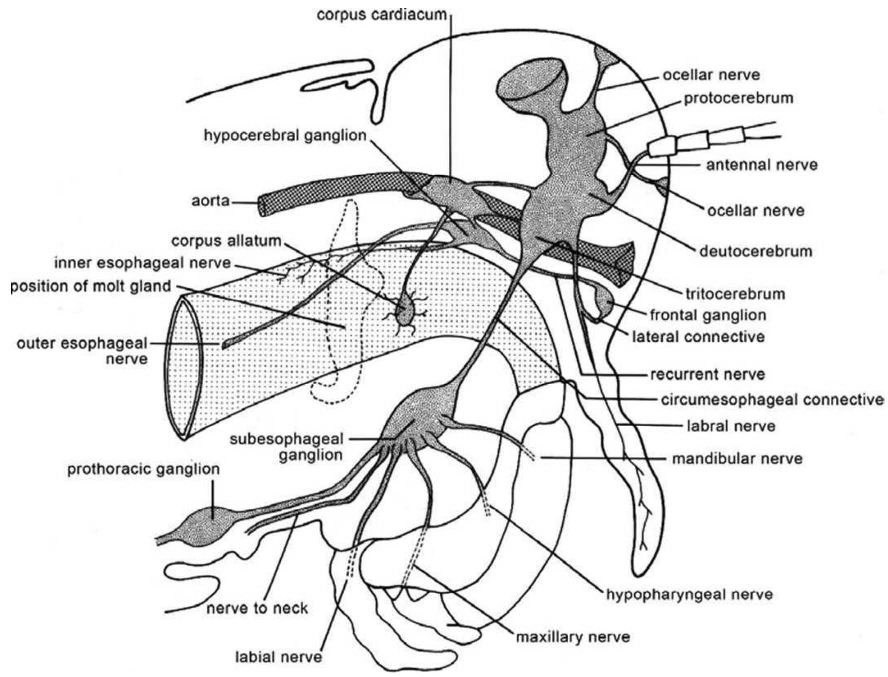

Fig. 2.13 *Lateral View of Anterior Central Nervous System, Stomatogastric Nervous System and Endocrine Glands of Locust*

III. Peripheral Nervous System (PNS)

Peripheral Nervous System (PNS) includes an extremely delicate network of nerve fibres and multipolar nerve cells located in integument. The peripheral nervous system consists of all of the motor neuron axons that radiate to the muscles from the ganglia of the CNS and stomodeal nervous system. The largest fibres of this network are derived from the paired nerves of the central nervous system.

Some of processes of the nerve cells are continuous with those of bipolar nerve cells whose terminal projections innervate sensory hairs on body surface. It has sensory neurons of cuticular sensory structures (sense organs) that receive mechanical, chemical, thermal or visual stimuli from an insect's environment.

2.3.3 Physiology of Nervous System

An insect's nervous system receives stimuli of different types from external environment and from within its own body. Response of insect depends on net assessment of these stimuli within central nervous system. The processes of receiving, assessing and responding to stimuli are known as **neural integration**. Neural integration involves impulse transmission along axons and across synapses, reflex pathways from sense organ to effector organ and coordination of these events within central nervous system.

I. Impulse Transmission

A nerve impulse is the conveying of a coded signal from a neuron to an effector (muscle cell, gland cell or another neuron) in response to a stimulus. This signal is transmitted along axon of neuron, bringing a *message* that instructs an effector to act. For example, in neuromuscular junction, nerve impulse moves along axon of a neuron to instruct a muscle cell to contract. In insects, impulse transmission or conduction occurs through two mechanisms namely axonal and synaptic impulse transmission.

i. Axonal Transmission

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Ionic composition varies between inside and outside of axon resulting in excitable conditions. It leads to impulse conduction as electrical response that is called action potential (Refer Figure 2.14). It takes place in following steps:

- In resting condition (polarized state) due to presence of abundant sodium ions (Na^+) outside, outer membrane is charged positively and inner membrane is charged negatively. This is due to movement of sodium ions from axoplasm (cytoplasm within axon) to outside of axons. The outward flow of sodium ions is known as **sodium pump**. On the other hand the potassium ions are more abundant in axoplasm.
- Upon stimulation by an external stimulus permeability of membrane is charged and flow of sodium ions stops. This causes movement of sodium ions inside axons and depolarization of membrane takes place. Flow of sodium ions inside is very fast causing inner membrane positively charged and outer part of membrane is charged negatively. Thus, it is propagating a short electro chemical current or impulse along the axon known as **action potential**.
- The period of permeability to sodium ions is short lived and is followed by a period of increased permeability to potassium ions. As a result of which the potassium ions flow outside axon, negatively charges inner membrane. This is called as **falling phase** of action potential. In this way nerve impulse are propagated in axons.
- As impulse passes in forward direction, permeability of membrane assumes original state, i.e., polarized condition due to decreased flow of potassium ions outside axons as a result of which repolarization takes place.

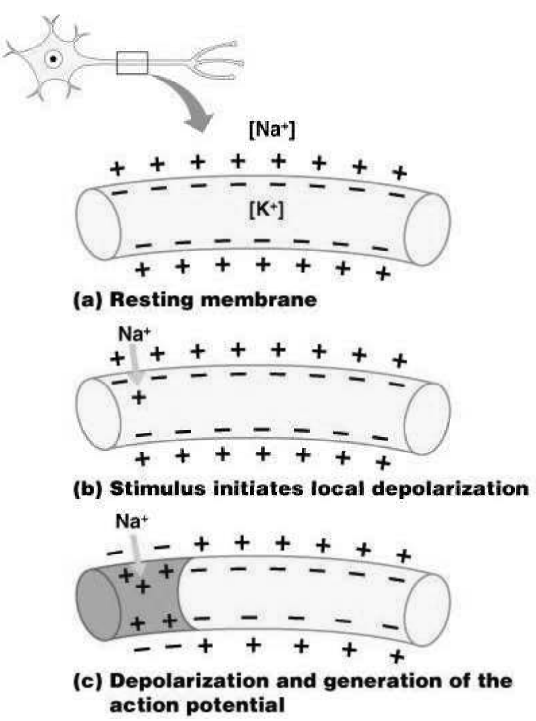

Fig.2.14 *Axonal Transmission of Impulse in Nerves*

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ii. Synaptic Transmission

Neurotransmitters are the chemical involved in impulse conduction through synaptic gap. When an impulse has passed along an axon it must cross the synapses in order to stimulate another neuron. Transmission across synaptic gap takes place through a neurotransmitter stored in synaptic vesicles. This neurotransmitter is Acetylcholine (ACH) (Refer Figure 2.15). It takes place in following steps:

- As soon as the impulse reaches terminal end of axon, synaptic vesicle fuse with membrane of axon, intermediate wall dissolve and neurotransmitter is released into synaptic gap.
- Acetylcholine comes in contact with post synaptic terminal of next neuron having Acetylcholine (ACH) receptors. Now ACH molecules bind with ACH receptors present on post synaptic terminal. It changes permeability of membrane causing depolarization and this initiates propagation of nerve impulse. In this way, impulses caused by external stimuli reach from one neuron to next neuron via axon through synapses.
- After synaptic transmission the ACH is hydrolyzed into acetic acid and choline by action of an enzyme called Acetyl Cholinesterase (ACHE). In this way, the ACH receptors become unoccupied in order to receive second message. Therefore in synaptic transmission, neurotransmitter Acetylcholine (ACH) acts as stimulus to receptor axons.
- Neurotransmitters and reactions help in impulse conduction is as follows:

Acetyl CO-A + Choline (choline acetylase) → Acetyl choline

Acetyl choline + Water (Acetyl choline esterase) → Choline + Acetic acid

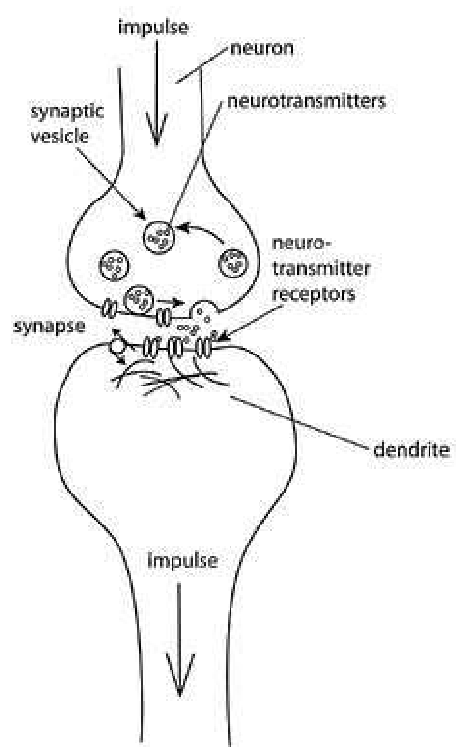

Fig. 2.15 *Synaptic Transmission of Impulse*

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II. Response to Nerve Impulse

Eventually, an impulse reaches effector organ, most commonly muscle. There is a fluid-filled space between tip of motor axon and muscle cell membrane called a **neuromuscular junction**. To achieve depolarization of muscle cell membrane and ultimately, muscle contraction, a chemical released from tip of axon diffuses across neuromuscular junction. In insect skeletal muscle, this chemical is L-glutamate. In visceral muscles, glutamate and serotonin are neurotransmitters.

III. Reflex Response

Reflex response is a sudden and involuntary response to stimulus. In insects reflex responses are segmental, that is a stimulus received by a sense organ in a particular segment initiates a response that travels via an interneuron located in that segment's ganglion to an effector organ in the same segment. For example, touching the tip of isolated ovipositor in silkworm, initiates egg-laying movements, suggesting that terminal ganglion of ovipositor and its nerves are intact.

2.3.4 Nervous System of Different Insects

Following is the description about nervous system of different insects:

I. Cockroach

Nervous system of cockroach is basically divided into three parts, i.e., as follows: central, peripheral and visceral (sympathetic) nervous systems (Refer Figure 2.16).

i. Central Nervous System (CNS)

It consists of **brain** and **ventral nerve cord** with its ganglia.

- **Brain:** Brain or supraoesophageal ganglion is a large and bilobed mass situated in head above oesophagus. It has three pairs of ganglia of head area fused together. It is divided into three areas: protocerebrum, deuterocerebrum and tritocerebrum. Rest of the three pairs of ganglia of head fuse to form sub-oesophageal ganglion which lies below esophagus. Brain and suboesophageal ganglion are connected together, on either side of oesophagus, via a circumesophageal commissure. Mushroom bodies in cockroach have double calyces having three concentric rings of neuropiles namely lip, collar and basal ring.
- **Ventral Nerve Cord:** From subesophageal ganglion runs posteriorly a double ventral cord along mid-ventral line of thorax and abdomen. It has 9 ganglia: 3 ganglia in thorax and 6 in abdomen. The last abdominal ganglion is the largest and is formed from many fused ganglia of posterior abdominal segments.

ii. Peripheral Nervous System (PNS)

The nerves given off from ganglia to all parts of body, constitute the peripheral nervous system. Protocerebrum of brain gives off paired optic nerves to eyes, deuterocerebrum gives off paired optic nerves to antennary nerves to antennae, and tritocerebrum supplies nerves to frons and labrum. Subesophageal ganglion supplies mandibular, maxillary and labial nerves to mandibles, maxillae and labium, respectively. Nerves from thoracic ganglia innervate thoracic muscles, chiefly those of wings and legs. First 5 abdominal ganglia send nerves to dorsal and ventral muscles of body wall, spiracles and heart. Whereas, last abdominal ganglion supplies nerves to muscles of last three abdominal segments, reproductive organs, copulatory appendages and anal cerci.

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iii. Visceral Nervous System

It has four ganglia and a retrocerebral complex as following:

A **frontal ganglion** lies above pharynx in front of brain. It sends nerves to pharynx, clypeus and labrum. It is connected to protocerebrum of brain via a median nervous connectives and to tritocerebrum via a pair of frontal connectives. Frontal ganglion is also connected via, a median unpaired recurrent nerve with a **hypocerebral ganglion** on oesophagus. It sends an oesophageal nerve, to **ingluvial ganglion** situated on crop. Branches from oesophageal nerve innervate salivary glands and their ducts. From ingluvial ganglion arise two nerves, one dorsal and other ventral to crop, that run posteriorly and get connected with a **proventricular ganglion** on surface of proventriculus.

Retrocerebral complex is situated above the hypocerebral ganglion. It is consist of two paired masses, the corpora cardiaca and corpora allata and related connectives. Corpora cardiac is neurosecretory and regulates heartbeats and peristalsis of foregut. Corpora allata produces hormones which help in reproduction and metamorphosis.

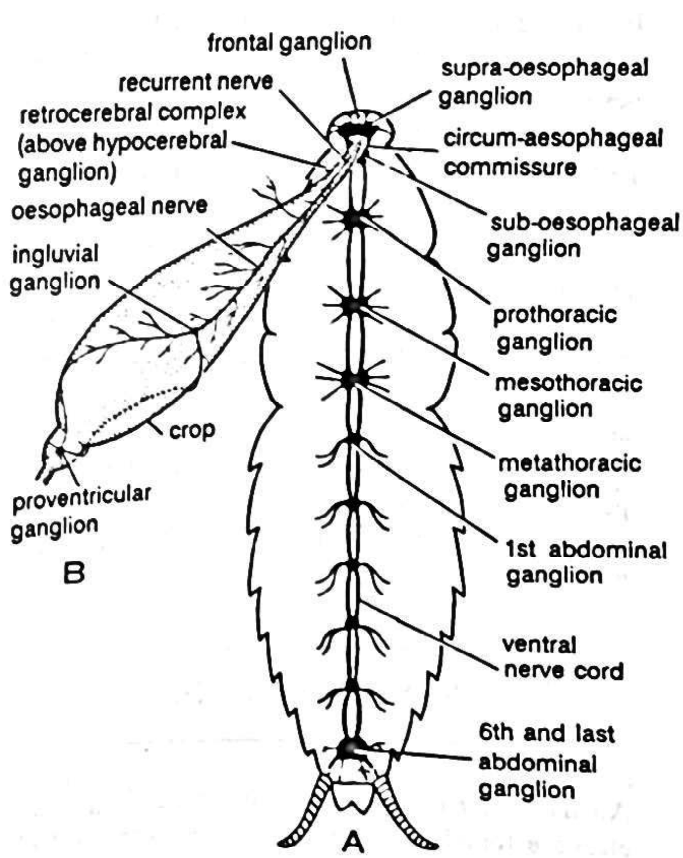

Fig. 2.16 *A. Central and Peripheral Nervous System in Cockroach; and B. Stomatogastric Nervous System*

II. Honey Bee

In a generalized embryo, there may be seven head ganglia, three thoracic, and at least ten abdominal ones. In the adult, however, many of these fuse with one another. In the head, for example, in place of seven ganglia there are only two, one situated above esophagus, called brain and one situated below it, called as subesophageal ganglion. Connecting cords are known as circumesophageal commissures.

- **Brain:** The brain of bee is distinctly composed of two parts. Protocerebrum have large optic lobes. Deutocerebrum consists principally of conspicuous antennal lobes that give off large antennal nerves. The tritocerebrum is not present as a distinct brain division and its nerves, the labral and the frontal commissures, arise from deutocerebrum at base of antennal lobes (Refer Figure 2.17 A and B).

  Mushroom bodies are most highly developed in bee. Mushroom bodies of bee have double calyces that contain three concentric rings of neuropiles called as lip, collar and basal ring. Their size is also large associated with learning behaviour and memory of foraging worker bee.

- **Sub-Esophageal Ganglion:** It consists of at most four ganglia which innervate mandibles, hypopharynx, first maxillae and labium or second maxillae.
- **Stomatogastric Nervous System:** A pair of nerves which unite in a small swelling called frontal ganglion. It lies between the pharynx and front of the head. A nerve runs posteriorly from this on dorsal side of pharynx or esophagus to behind the brain. This nerve divides into several branches, some of which bear small ganglia while others extend backward on esophagus to stomach. These nerves are the stomatogastric system also called sympathetic system.
- **Ventral Nerve Cord:** It is divided in two parts, i.e., as follows:
  - **Thorax Ganglia:** In thorax of bee (Refer Figure 2.17) there are two large ganglia (1Gng and 2Gng). The first is prothoracic and it innervates prothorax and first pair of legs. The second is situated in front of middle legs and is a combination of mesothoracic and metathoracic ganglia and first two abdominal ganglia. This composite structure formed as it innervates middle and hind legs, the bases of both pairs of wings, mesothorax, metathorax, propodeum and first abdominal segment (true second segment) behind constriction (petiole).
  - **Abdominal Ganglia:** The first and second ganglia of abdomen (Refer Figure 2.17) 3Gng and 4Gng lie in the first two segments (true II and III abdominal segments) behind constriction. The nerve trunks of these ganglia also innervate segments III and IV. The next three ganglia (5Gng, 6Gng and 7Gng) lie in segments they innervate V, VI and VII abdominal segments. The last seventh ganglion (7Gng), supplies all of segments behind it with nerves. Therefore, seventh ganglion is a compound of ganglia belonging to seventh, eighth, ninth and tenth abdominal segments.

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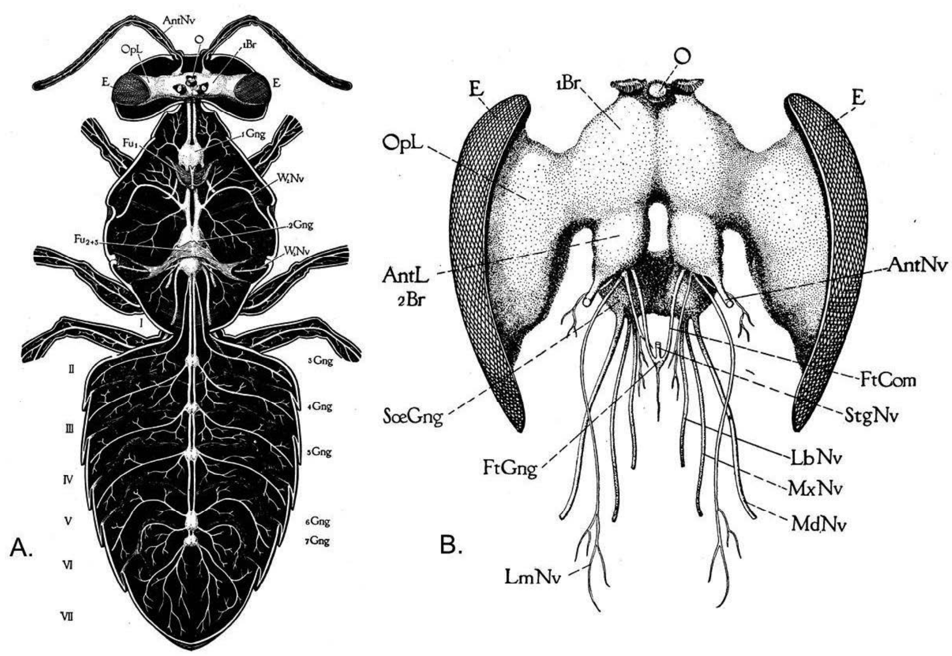

Fig. 2.17 *A. Nervous System of Worker Honey Bee, Dorsal View; and B. Brain and Suboesophageal Ganglion of Worker Honey Bee and their Principal Nerves, Anterior View*

In above Figure 2.17, following abbreviations are used which means as follows: 1Br-Protocerebrum, 2Br-Dueterocerebrum, AntNv-Antennal Nerve, AntL-Antennal lobe, OpL-Optic Lobe, SoGang-Subesophageal ganglion, E-eye, O-Ocelli, 1Gng-7Gng-Segmental ganglion, WNv-Wing Nerve, *StgNv*-stomatogastric trunk, labral nerve-LmNv, MdNv, MxNv, and LhNv- mouth parts nerve, frontal ganglion=FtGng.

Check Your Progress

8. What is nervous system?
9. Name the types of cells in nervous system.
10. Distinguish between the function of neurons and glial cells.
11. What is cell body present in neuron?
12. What are axon terminals?
13. Define the term synaptic cleft.

2.4 VISUAL ORGANS IN INSECTS

Eye is visual organ or photoreceptor and capable of recording form, colour differences or movements in external objects. Insect eyes are always located on the head and the optic centers lie in protocerebral parts of brain.

Insect visual organs fall into three groups as dorsal ocelli, lateral ocelli (stemmata) and compound eyes (Refer Figure 2.18). Some insects also have epidermal light receptors and in some insects, light have a direct effect on cells in the brain.

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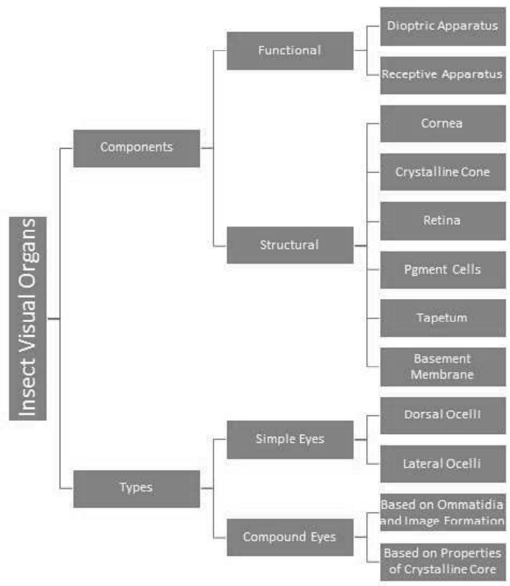

Fig. 2.18 *Components and Types of Visual Organ in Insects*

In exopterygote insects, young (larvae or nymphs) resemble adults but have externally developing wings. They undergo modest change between immature and adult, without going through pupal stage. This is called hemimetabolism or incomplete metamorphism. Examples are cockroaches, termites and grasshoppers.

Endopterygote insects, also known as Holometabola, develop wings inside body and undergo an elaborate metamorphosis involving a pupal stage. This is called as **holometabolism** or **complete metamorphism**. Endopterygota or holometabola have larval and adult stages differing greatly in their structure and behaviour. Examples are butterflies, bees, wasps and flies.

2.4.1 Structure of Various Visual Organs

Structure of various visual organs of insects is discussed below:

General Components of Visual Organs

In each visual organ, there are two functionally distinct parts namely, a dioptric apparatus and a receptive apparatus.

- **Dioptric Apparatus:** Dioptric apparatus transmits and condenses impinging light rays upon receptive surface. It always includes cuticle in the form of lens, largely formed by specialized cells of optic epidermis.
- **Receptive Apparatus:** Receptive apparatus consists of sensory cells forming retina, which present specialized receptive surfaces at points where light rays are focused and are continued directly into optic nerve.

There are basically two kinds of eyes namely **simple** and **compound eyes**. Simple eyes and compound eyes are not fundamentally different in their structure. A simple eye or ocellus, is a photoreceptor having a single dioptric apparatus for all sense cells. A compound eye has numerous groups of sense cells and a separate dioptric apparatus for each group. Anatomically, an insect's organ of vision has various components. These components are cornea (or corneal lens), corneagenous cells, crystalline body, retina, rhabdom and rhabdomeres, pigment cells, tapetum and basement membrane. Features of these components vary with kind of insects eyes which are explained under following sections:

I. Simple Eye

Simple eyes are divided into two categories, i.e., as follows:

- Dorsal or primary ocelli of adult insects and nymphs.
- Lateral ocelli or stemmata which are larval eyes.

i. Dorsal Ocelli

The dorsal ocelli (singular ocellus) are simple eyes of adult insects in addition to compound eyes and of exopterygote larvae and nymphs. Typically there are three ocelli: one median, located on upper part of frons or the frontal area of head and other two located more lateral on postfrontal region. Thus, they appear in a triangle. The dorsal ocelli are innervated from ocellar lobes which are positioned in protocerebrum, between mushroom bodies.

Structure of Dorsal Ocelli

The dorsal ocelli (Refer Figure 2.19A) greatly vary in the details of their structure in various insects, but they have some common vital structures that are explained in following points:

- In dorsal ocelli, corneagenous cells and retinal cells form two distinct layers. Corneagenous layer placed between cornea and retina. The corneagenous cells are transparent so as to impede transmission of light to retinal cells.
- Cornea (or corneal lens) is cuticular covering of eye, which is always transparent so as to allow light rays but is of sufficient thickness to exclude harmful ultraviolet. The cornea is a simple dome over eye. But generally it is thickened to form a strongly biconvex lens.
- When a corneal lens is developed, corneagenous cells are become small and appear as a vitreous epithelium below the lens.
- In absence of a corneal lens, corneagenous cells may be enlarged to form a crystalline dioptric body. In some cases a vitreous mass of refractive fluid occurs between epithelial corneagenous cells and retina cells.
- Peripheral or pigment cells of corneagenous layer, where corneagenous cells merge into normal epidermis, usually contain a dark pigment forming an iris about the sensory elements.
- Visual or retinal cells are in groups of two, three or more cells. Each group is called as a retinula that surrounds a longitudinal optic rod or rhabdom. Rhabdoms produced by adjacent retinal cells are present in outer part of retina. Retinal cells are usually pigmented. There are supporting cells scattered between sensory cells of retina that mechanically supports to structure of eye.
- A tapetum is formed in some ocelli by a sheet of connective tissue through base of retina containing light-reflecting substances.

ii. Lateral Ocelli

Larvae of endopterygotes (holometabolous) have lateral ocelli as their only visual organ. Lateral ocelli are also called stemmata (singular: stemma). As their name suggests, they are situated on sides of head. They occupy positions in larval body where compound eyes of adult stage are formed.

Number Variations: Number of lateral ocelli varies with insect species and not always constant in same insect species. For example, in some groups there is a single ocellus present on either side while in others there may be 6, 7 or more ocelli.

Developmental Significance: Absence of compound eyes in holometabolous larvae is due to development of these organs being delayed until their pupal stage. Thus, their places are taken by lateral ocelli which are adaptive organs and functional during larval instars.

Types of Lateral Ocelli

There are two kinds of lateral ocelli; one is having a single rhabdom, and another has many rhabdoms. Lateral ocelli with single rhabdom found in Larvae of Scorpionflies (*Mecoptera*), Lacewings (*Neuroptera*), Caddisflies (*Trichoptera*) and Butterfly (*Rhopalocera*). Lateral ocelli having multiple rhabdoms are present in larvae of Sawflies, Ground and Aquatic beetles.

Structure of Lateral Ocelli

Lateral ocelli differ from dorsal ocelli as the fact that they are innervated from optic lobes of brain. In their simpler forms and in their growth, lateral ocelli do not differ from dorsal ocelli. Each is developed by differentiation of cells in ocular region of epidermis into a corneagenous layer and a retinal layer. Structure of lateral ocelli exhibits great variations.

The cornea is flat or dome shaped but usually it forms biconvex lens. Corneagenous cells form a thick vitreous layer between lens and retina. Usually, there is a dioptric body below cornea. Dioptric body is either made of vitreous corneagenous cells or produced as a vitreous secretion of cells. Rhabdoms are generally present in outer part of retina. Rhabdoms are formed in usual manner between distal ends of retinal cells. Pigment is variously distributed in eye or sometimes absent (Refer Figure 2.19B).

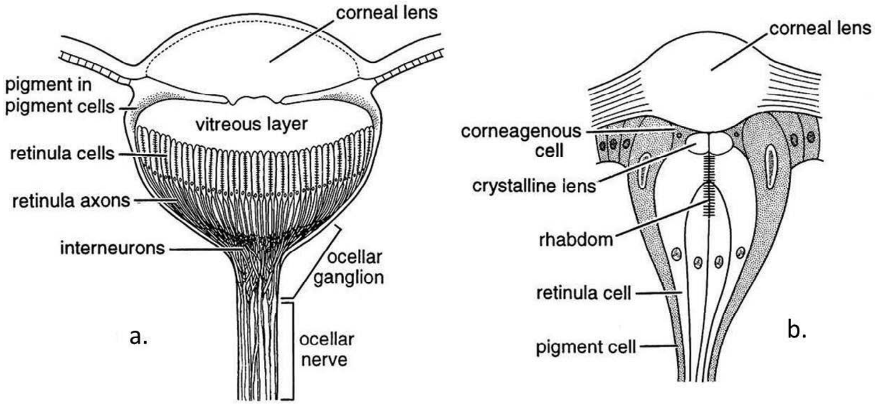

Fig. 2.19 *L.S. through Simple Eyes; A. Light-Adapted Median Ocellus in a Locust; B. Simple Stemma in a Butterfly Larva*

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II. Compound Eyes

The compound eyes are principal visual organs of insects. Generally, they occur in adults of winged insects and nymphs of hemimetabolous insects. Compound eyes are named so as they are built from several similar units known as ommatidia (singular: ommatidium). Each compound eye comprised of many thousand ommatidia. For example, there are about 30,000 ommatidia present in eyes of dragonflies, 10,000 found in drone honeybees, 5500 in worker honey bees and 800 in *Drosophila*.

Structure of Ommatidia

Each ommatidium made of an optical, light-gathering component (also called dioptric apparatus) and a sensory component (receptive apparatus). Light-gathering component includes corneal lens plus crystalline cone. Primary sense cells are retinula or retinular cells that collect and convert light into electrical energy. It has various enveloping cells which are pigment or iris cells (Refer Figure 2.20 A and B and Figure 2.21C). Followings are the detailed components of ommatidium,

Corneal Lens (Cornea or Lens): Cuticle encasing eye is transparent, colorless and generally forms a biconvex corneal lens. Each corneal lens is formed by two epidermal cells termed as corneagenous cells. Afterward these cells become withdrawn to sides of ommatidium and produce primary pigment cells.

Crystalline Cone: The crystalline cone is a clear, hard material. Below the cornea are four cells termed as Semper cells. Semper cells in several insects form a second lens called as crystalline cone. Crystalline cone is generally a hard, clear and intracellular structure surrounded laterally by primary pigment cells.

Retinula, Rhabdom and Rhabdomere: Cylindrical group of elongate sense cells called **retinula** or **retinular cells** enclosing a long axial rhabdom. There are eight retinular cells occur below crystalline cone. One of these cells is usually degenerate or eccentrically located. The seven remaining cells are arranged around a central axis. Mature sensory cells are unipolar. Their inner surface is modified to form a receptive area called **rhabdomere**. Collectively, rhabdomeres form a **rhabdom**. Rhabdomeres has closely packed microvilli which extend from cell surface. In cross section, the microvilli are hexagonal. Rhabdom contains rhodopsins as visual pigments that resemble those of vertebrate eye. Retinular cells are sensory components and thus form longer photoreceptor neurons. Its narrowed inner ends penetrate basement membrane of eye and become fibers (axon) of optic nerve.

Type of Rhabdom: Rhabdom can be of open and closed types (Refer Figure 2.20 C and D). In open type, found in flies and bugs, individual rhabdomeres are physically separated and each serves as an optical waveguide. In closed type, common to most insects, rhabdomeres are wedge-shaped and closely packed around central axis. In a closed rhabdom, rhabdomeres function collectively as a single waveguide.

- **Primary Pigment Cells:** Each ommatidium is enclosed in a sheath of cells containing an abundance of dark pigment. Corneagenous pigment cells are often termed primary pigment cells of iris.
- **Secondary Pigment Cells:** Surrounding photosensitive cells are secondary pigment cells which, like primary pigment cells, contain granules of red,

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yellow, and brown/black pigments (mainly ommochromes).

- **Tapetum:** A reflecting surface called as tapetum and is differently developed in different eyes. It gives greater efficiency to small amounts of light and is more usually present in nocturnal species. It reflects light from depth of eye back into retina and gives a shining appearance to eyes of many insects when seen in dim light. In compound eyes, tapetum consists of dense masses of glistening air-filled tracheae that penetrate between retinal elements. Thus form a reflecting sheath enclosing each group of retinal cells.
- **Basement Membrane:** Inner surface of eye is always covered by basement membrane continuous with that of surrounding epidermis. The membrane is penetrated by processes of retinal cells, which become fibers of optic nerve.

Types of Compound Eyes

Following are the types of compound eyes:

i. Based on Ommatidia and Image Formation

Two ommatidial types namely photopic and scotopic are found according to arrangement of retinular and pigment cells. The sensory receptor (retinular) cells of diurnal (active during day) insects terminate near to lens, and, due to way of image formation, these are known as **apposition eyes** (Refer Table 2.2). Night-flying insects have eyes with a clear zone between lenses and sensory components (rhabdom) and thus they are termed as superposition eyes and form brighter images than apposition eyes. Scotopic (superposition) (Refer Table 2.2) ommatidia have short retinular cells whose rhabdom is connected to crystalline cone by a translucent filament that serves to conduct light to rhabdom. The secondary pigment cells do not envelop retinular cells and their pigment granules are capable of marked longitudinal migration Thus it allows light from adjacent ommatidia to reach each rhabdom, enhancing rhodopsin activation.

Table 2.2 *Difference between Apposition and Superposition Eyes*

S.No.	Apposition Eyes	Superposition Eyes
1.	Due to apposition image formation.	Due to superposition image formation.
2.	These eyes have photopic (apposition) ommatidia.	These eyes have scotopic (superposition) ommatidia.
3.	It is found in diurnal or day flying insects, for example bees.	It is found in nocturnal or night flying insect, for example butterflies and beetles.
4.	Retinular cells (rhabdom) occupy distance between crystalline cone and basal lamina.	These have short retinular cells (rhabdom) and form clear zone between rhabdom and crystalline cone.
5.	Secondary pigment cells lie alongside retinular cells.	Secondary pigment cells do not envelop retinular cells.
6.	Pigment does not migrate longitudinally.	Pigments are capable of migrating longitudinally.
7.	Does not form brighter images.	Form brighter images than apposition eyes.
8.	Rhabdoms convey an erect mosaic image built up of adjacent sharing from all ommatidia.	Superposition eye produces a single upright image.

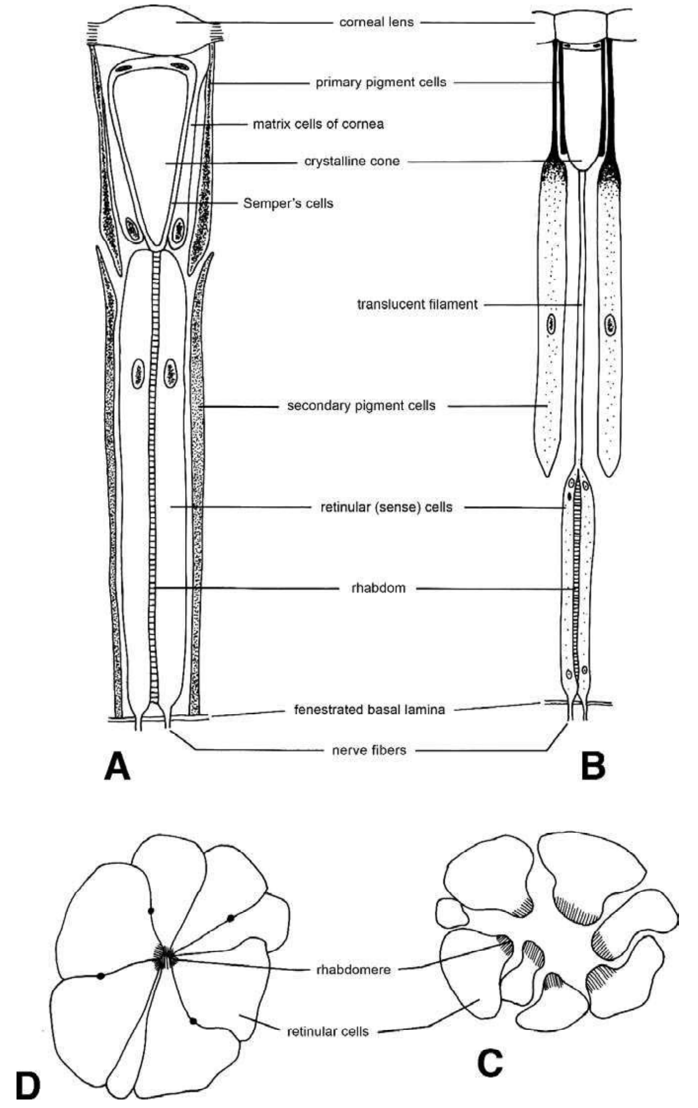

Fig. 2.20 *A. Photopic Ommatidium, B. Scotopic Ommatidium, C. Open Rhabdom; and D Closed Rhabdom*

ii. Based on Properties of Crystalline Cone

Four types of compound eyes are described among insects on the basis of crystalline cone:

- **Eucone Eyes:** In eucone eyes each ommatidium contains a true crystalline cone, which is a hard refractive body formed as an intracellular product of cone cells. Examples of eucone eyes are locust, dragonflies, butterflies, bees and some bugs.
- **Pseudocone Eyes:** In pseudocone eyes type of eye, there is no true crystalline cone and the four cone cells are filled with a transparent, semiliquid material. Examples of pseudocone eyes are Muscoid flies, short-horned flies.
- **Acone Eyes:** In acone eyes, there is a group of elongate, transparent cone cells but the latter do not secrete any kind of cone whether crystalline or liquid. Examples of acone eyes are Mosquito, Earwig, true weevils, ladybugs.

- **Exocone Eyes:** In exocone eyes, crystalline cone is replaced by a cone of extracellular, cuticular material which appears as a deep ingrowth from inner of corneal facet. Examples of exocone eyes are skin beetles, click beetles and pill beetles.

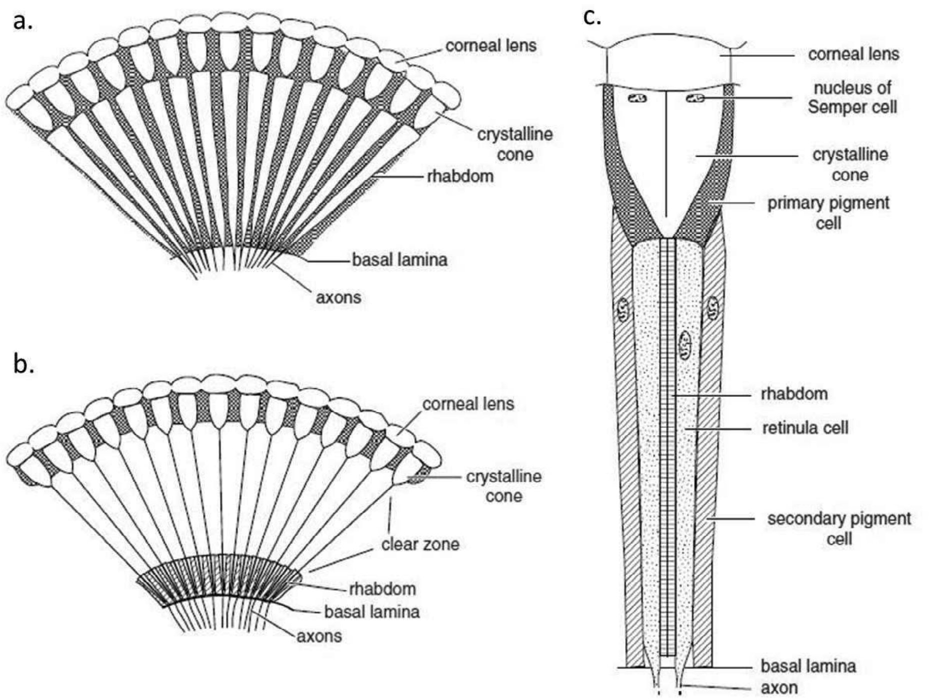

***Fig. 2.21** Diagrammatic Representation of A. Section Across Apposition Eye Exhibiting the Rhabdoms Extending to Crystalline Cones, B. Section Across a Superposition Eye Exhibiting the Clear Zone Between Rhabdoms and Lens Systems and; C. T.S. of Single Ommatidium*

2.4.2 Functions of Various Visual Organs

Following are the functions of compound eyes and ocelli:

I. Functions of Compound Eyes

- **Resolution**: Resolution refers to degree of fineness with which an eye forms an image of an object. In compound eyes, resolution is measured by interommatidial angle. This angle is angular separation of visual axes of nearby ommatidia. In apposition eyes where each rhabdom functions as a unit, fineness of image will be greater when smaller is interommatidial angle. This angle is greater than 5^o in many beetles and as small as 0.24^o in eye of dragonfly. High resolution is needed in predatory insects such as dragonflies and robber flies.
- **Form Perception:** The eye's ability to detect form of an object depends on its resolving power. In predatory insects, such as Mantids (*Mantodea*), acute zone provides a region of high-quality form perception in front of eye where prey is detected before predator attack.
- **Field of View:** Insects with well-developed compound eyes generally have an extensive field of view. For example, in horizontal plane Cockroach has

vision through 360^o, with binocular vision in front and behind head.

- **Distance Perception:** Insects are able to judge distance with considerable accuracy. This is most common in grasshoppers, which jump to a perch, or in predators like Mantids, but is also true for any insect landing at end of a flight.
- **Visual Tracking:** Visual tracking refers to an animal's ability to keep a moving target within a specific area of retina, and also when animal itself is moving. It happens, for example in predator, such as a mantis or dragonfly when they catch its prey, or when a male fly chases a female.
- **Color Vision and Light Sensitivity:** Light sensitive cells do not respond equally to all wavelengths of light. Rather, they are sensitive to some parts of spectrum. Some insects show very significant phototaxes (behavioural responses to light). Some insects, such as ants are negatively phototactic to Ultraviolet (UV) rays and when given a choice will always congregate in a region not illuminated by UV. Worker bees are attracted to yellow and red flowers by pattern reflection of UV. All butterfly eyes have three distinct rhodopsins, sensitive to UV (360 nm), blue (470 nm), and green (530 nm).
- **Sensitivity to Polarized Light:** Sunlight entering Earth's atmosphere is filtered, that is, light rays in some planes are reflected by dust particles, etc. Thus light striking Earth's surface is partially polarized. Many insects such as bees, ants, crickets, locusts and some beetles can detect and make use of plane of polarization for navigation and orientation.

II. Functions of Ocelli

The principal function of ocelli appears to be horizon detection as a component of horizontal flight. Though for some insects the ocelli may provide information on sudden changes in light intensity. It serve as a general stimulus to the nervous system, initiate specific phototaxes (response to light), and detect the plane of polarized light. Stemmata have functions similar to those compound eyes.

2.4.3 Physiology of Vision

The fully developed eyes of insects are dividable into two parts namely dioptric part and perceptive or receptive part that are different with respect to their structures and physiology.

Before understanding physiology of insect eyes, following terms are necessary to understand:

- **Reflection:** When a ray of light comes back into the same medium after striking the surface of another medium then the phenomenon is called reflection of light.
- **Refraction:** The change of direction and speed of light as it enters from one medium to another is termed as refraction of light. Examples of refraction are lenses, prism and telescope.
- **Single Mosaic Image:** A *mosaic* is a combination or merge of two or more *images*.

- **Inverted Image**: Inverted image means the image is upside down compared to the object.
- **Upright Image:** An erect image appears right-side up. The word erect means upright or straight. Hence, an image formed by a mirror or a lens is said to be an erect image if it is upright, i.e., not inverted.

  Vision Mechanism of Ocelli and Compound Eyes

  Vision Mechanism of ocelli and compound eyes is discussed below:

Vision Mechanism of Ocelli: Dorsal ocelli are built upon a plan just similar to that of the human eye than insect compound eye. Because there is no power of accommodation in dioptric layer and lens is intensely biconvex, vision is restricted to perceptivity of very close objects. A few numbers of visual components involves an image of a crude or indefinite type and this image is an inverted form. Ocelli are used to differentiate among light and darkness and are able to convey a coarse image of just very close objects.

Vision Mechanism of Compound Eyes: In compound eye each ommatidium will only convey to retinula, rays coming from a very small part of entire field of vision, and just those travelling in direction of its axis. Impression perceived by compound eye would be a single mosaic image, produced by same number of points of light as there are ommatidia. Each point of light depending on colour and density to related part of object viewed.

Images Formation by Apposition Eye and Superposition Eye

Formation of images by apposition eye and superposition eye is discussed below:

Formation of Images by Apposition Eye

Each of ommatidia in apposition eye is different from adjacent ommatidia in having screening pigment, so as to each act as an independent unit. Each lens forms a small inverted picture of an object in its field of view, which is in focus at tip of rhabdom. Since, rhabdoms of apposition eyes are fused, they act as light guides, within which image feature is vanished and all photoreceptor cells from one ommatidium contribute same small field of view. Light reaching rhabdom in each ommatidium has an overall intensity that differs from one ommatidium to next, based on portion of light reflected by objects in field of view. Thus, altogether rhabdoms convey an erect mosaic image built up of adjacent sharing from all ommatidia (Refer Figure 2.22A).

Formation of Images by Superposition Eye: The superposition eye produces a single upright image. This needs that light is refracted not only on entering each lens, but also within it, so as to follows a curved pathway. The lenses in superposition eyes each have a gradient of refractive index from the lens axis to its margin (Refer Figure 2.22B). This gradient leads light rays to go through greater refraction as they travel toward the lens axis, and a smaller amount of refraction since they travel away from the axis, therefore creating the light path curved. The outcome of this is to bend light continuously as it runs down the lens, and the entire structure acts as though it were a two-lens telescope, receiving parallel light, focusing it internally and then releasing it again as a redirected parallel beam of light.

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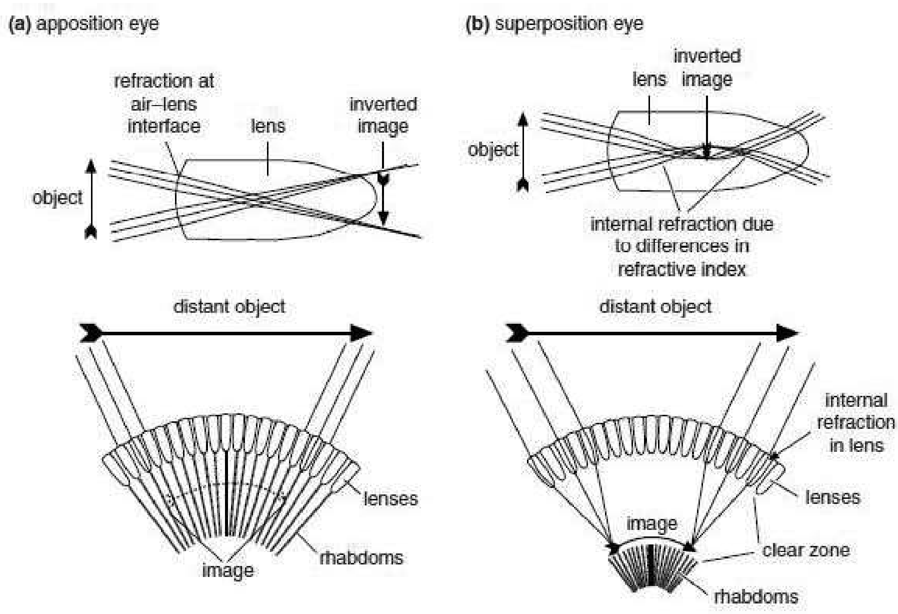

Fig. 2.22 *A. Image Formation in an Apposition Eye; and B. Image Formation in a Superposition Eye*

In above Figure 2.22 image formation in an apposition eye is shown where the information about object is represented as a sequence of dots differing in intensity presented by dotted arrow and image formation in a superposition eye is shown where light rays are refracted internally within lens. They are unfocused as they exit lens, but together form a single upright image at tips of rhabdoms.

Transduction

Transformation of light to electrical energy involves visual pigment rhodopsin. Phototransduction cascade leads to transformation of rhodopsin to active metarhodopsin. Metarhodopsin is self-photosensitive, absorbing light at a different wavelength from rhodopsin that produces it. For example, the chief rhodopsin in flies absorbs at 480 nm and converted metarhodopsin absorbs at 560 nm. Photoactivation retransform metarhodopsin to inactive rhodopsin.

Visual Organs of Different Insects

Visual organs of cockroach and honey bee are discussed below:

Cockroach

In cockroach visual organs are of two kinds namely **compound eyes** and **ocelli**.

i. **Compound Eyes:** Compound eyes are a pair of large, sessile, compound eyes in the form of black, kidney-shaped organs on lateral sides of head. Each consists of about 2,000 visual elements or units, called ommatidia.

Compound eye of cockroach and other insects is a very elaborate structure. The pigment does not seem to be retractable in eyes of cockroach. Owing to its form and permanently extended pigment sheath, the only light rays which reach the retinular cells are those nearly parallel to its long axis. Thus, the image seen by whole eye is made up of many spots of light, each contributed by one ommatidium.

This is known as a **mosaic** or **apposition image**. Compound eyes are specially adapted to perceive movements of objects.

ii. Ocelli: At the base of each antenna is a fenestra which represents a simple eye or ocellus. Each comprises of a single corneal facet. It is mainly concerned with light-collecting rather than image forming. Perhaps it enhances the sensitivity of compound eyes.

Honey Bee

Like many insects, bees have two different types of eyes-each with separate functions, i.e., **dorsal ocelli** and **compound eyes** (Refer Figure 2.23).

i. Dorsal Ocelli: The three smaller eyes in the center-top of a bee's head are called dorsal ocelli. These eyes have single lenses and help bee to maintain stability and navigate. They enable bee to judge light intensity and stay oriented. Using these ocelli, bees can gather light and see ultra-violet light, helping them to detect UV flower colors.

ii. Compound Eyes: Every bee has two large compound eyes. A compound eye is made up of thousands of tiny lenses called **facets**. Each of these facets takes in one small part of the insect's vision. The bee's brain then converts these signals into a mosaic-like picture made of each image. Worker bees have 6,900 facets in each eye, and drones have 8,600 facets. Every facet is connected to a tiny tube. Each of these units, called an ommatidium, contains a lens (facet), a cone of visual cells and pigment cells that help separate it from its neighbor cells.

A bee is able to see color, because each of these tiny tubes contains eight retinular cells that respond to light. Four of these cells respond to yellow-green light, two respond to blue light, and one responds to ultraviolet light.

Bees can use polarized light to locate direction even when sun isn't shining. They then communicate these directions to colony. Bees can find their way back home by checking the pattern of polarized light in the sky.

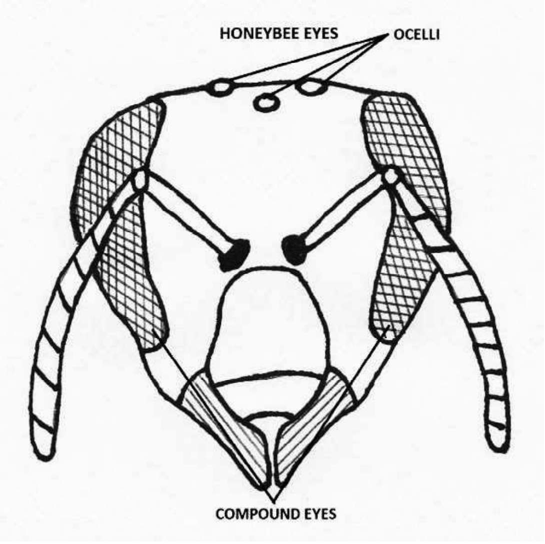

Fig. 2.23 *Eyes of Honey Bees (as in Many Insects)*

Check Your Progress

14. Define the term holometabolism.
15. Name the parts of visual organ.
16. Give the function of dioptric apparatus.
17. What does receptive apparatus consists of?
18. How many types of eyes are there?
19. What is a simple eye?
20. What are dorsal ocelli?
21. Distinguish between eucone eyes and pseudocone eyes.

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2.5 SOUND PRODUCTION IN INSECTS

Insects produce special sounds or receive these sounds through sense-organs and react to them with appropriate behaviour patterns. Sound is produced either by rubbing one part of body to another part or one part by other external object. A single insect species can make several sounds, each with its own function. Sounds and songs of different kinds and intensities are produced by a number of species in insects (Refer Figure 2.24). There are biological significance of these sounds in insect's behaviour and communication, i.e., as follows:

- Sound production facilitates mating by attracting sexes or stimulating female.
- In some cases, it can express sexual rivalry between males.
- It serves species-recognition thus helping to keep members of same species together.
- It communicates warnings of danger or has a defensive function.

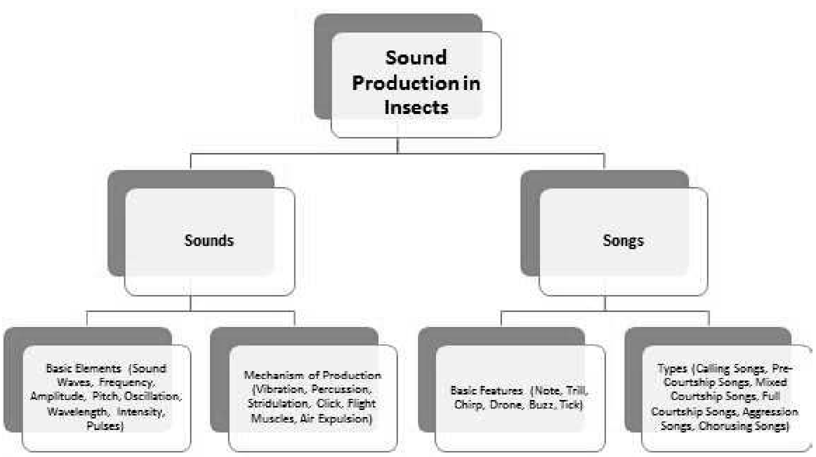

Fig. 2.24 *Sound Production in Insects*

Basics of Sounds

Sound is produced when an object's vibrations move through a surrounding medium (air, water, or solid). Sound travels in waves and are composed of compression

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and rarefaction patterns. Compression happens when molecules are densely packed together. Alternatively, rarefaction happens when molecules are distanced from one another (Refer Figure 2.25). Following terms are used to characterize sounds:

- **Frequency:** Frequency is number of sound waves produced each second. Hertz (Hz= cycles per second) is a measure of sound frequency.
- **Amplitude:** Amplitude of a sound wave determines its relative loudness.
- **Pitch:** Pitch refers to the quality that enables us to judge sounds as being higher and lower. A high-pitched sound causes molecules to rapidly oscillate, while a low-pitched sound causes slower oscillation.
- **Oscillation:** Oscillation is the movement back and forth in a regular rhythm.
- **Wavelength:** Wavelength is distance that wave travels before it repeats itself. Wavelength itself is a longitudinal wave that shows compressions and rarefactions of sound wave.
- **Intensity:** Intensity is power per unit area carried by a sound wave. The more intense the sound is, the larger the amplitude oscillations will be.
- **Pulses:** Sounds waves can be either pulse waves or periodic waves. A pulse wave defined as one assault to medium while periodic waves are series of successive assaults on medium.
- **Acoustic Signals**: Acoustic signals are noises (vibration, sound, etc.) that animals produce in response to a specific stimulus or situation, and that have a specific meaning.
- **Substrate Borne Vibrations:** Substrate can be the ground or a plant leaf or stem or the surface of water, or a spider's web or a honeybee's honeycomb. Animals or insects moving on these substrates typically create incidental vibrations that can alert others to their presence. Such vibrations are called substrate vibrations.
- **Air Born Vibrations:** Insects use airborne vibrations produced by their own body or body parts movements, for example wingbeats to control their behaviour and communicate with mates.

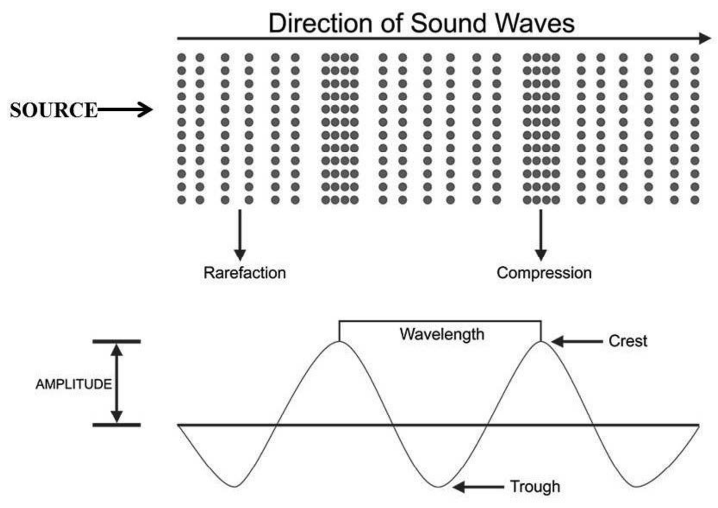

Fig. 2.25 Basic Features of Sound Waves

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2.5.1 Sound Producing Organs

Structures responsible for producing sound and auditory mechanism can include any part of insect's exoskeleton. Insects also have specialized structures, such as timbal (used in click mechanisms), scraper and file (used in stridulation). Several insect species have two sets of sound-producing organs, for example aquatic bugs or auditory organs, for example true crickets. Insect body parts and organs responsible for producing sounds are as follows:

- **Head Parts:** Mandibles in Locust, palpi in pygmy mole crickets, antennae in stick insects, head capsule in death-watch beetles,
- **Thoracic Parts:** Pronotum in longhorn beetles, mesonotum in click beetles, metanotum in Hump-winged Grigs.
- **Legs and Wings:** Forelegs in bush crickets, middle legs in Stag beetles, hind legs in Bess beetles,
- **Abdomen:** Many of abdominal segments in insects of beetles, grasshopper, aphids, and the cerci in cockroach.

2.5.2 Mechanism of Sound Production

There are basically five categories of sound producing mechanisms documented by Ewing (1989). These are as follows:

- Vibration
- Percussion
- Stridulation
- Click / Tymbal Mechanisms
- Flight Muscles
- Air expulsion

Details of these sound producing mechanisms are explained below:

i. Vibration

Sound produced from vibrations of relatively unspecialized parts of insect body. In most insects neuromuscular activity leads to mechanical vibration of some exoskeletal structure. These vibrations are transduced (either directly or indirectly) as cycles of compression and rarefaction to surrounding medium or a contacted solid substrate.

Abdomen and Leg Vibration: Most usually oscillations of abdomen, either dorso-ventrally or laterally produce vibration. This type of sound production is termed as **tremulation**. Such sounds are usually transmitted through legs to substrate on which insect is walking or standing. These are therefore usually detected as substrate transmitted vibrations. Such signals have been documented in various insects, but are well known in lacewing flies.

Wing Vibration: Vibrations of wings are most important in insect signalling. Oscillatory movement of wings of an insect sets up regions of compression and rarefaction and a vibrational sound is produced. Sounds are certainly produced as byproducts of flapping flight. Many insects have developed the use of wing vibrations in communication. The flight sounds in swarming mosquitoes are known often to be species-specific and to function in part, for species recognition. Low frequency wing vibration is used in courtship dances of fruit flies. When in close proximity, the pulsed songs of these flies stimulate antennal receptors of other individuals by air particle vibration in surrounding area.

Sensing Vibrations: Most insects detect sound with a **tympanic membrane** in abdomen such as grasshoppers and moths or in legs of crickets and katydids. Mosquitoes possess antennal hairs that resonate to some frequencies of sound. Sound vibrations can also travel through solid objects. Thus some insect such as ants, bees, termites, and treehoppers can sense **substrate vibrations** with mechanoreceptors such as chordotonal organs in their legs.

Substrate-borne communication occurs in insects such as bees, termites, ants, lacewings, stoneflies and beetles. Substrate vibration can be produced through percussion, stridulation and timbal mechanisms or through contractions of flight muscles, details of which are followed as:

ii. Percussion

Percussion refers to vibrations produced by effect of body part against substrate or by clapping two parts of body against each other. A single tap on a solid surface produces a complex wave pattern. Its spectral composition and propagation largely varies according to nature of solid. Substrate vibrations are more important for most insects using percussion for communication.

Many insects produce vibrational signals by striking unmodified parts of their body against objects in their environment. Some termites and beetles use their heads for this purpose. As an example, soldiers of Dampwood termites produce repeated series of taps by rocking their heads up and down and banging their mandibles on the ground and/or their dorsal heads against the roof of their galleries.

Booklice and some stoneflies of both sexes generate substrate vibrations through abdominal movements. Some species have small cuticular knob on ventral surface of abdomen, which they rhythmically drum against ground. Stoneflies and lacewings do not directly touch substrate with their abdomen, but rather transmit abdominal oscillations to ground via their legs.

iii. Stridulation

Stridulation refers to production of vibrations by moving a cuticular ridge on one body part over a toothed ridge on another. Cuticular ridge is called as scraper or plectrum and a toothed ridge is known as file or strigil. Repeated contacts of scraper against teeth of file cause body part to vibrate. These vibrations of insect's body give rise to substrate vibrations after transmission through the legs. If vibrating membrane is of appropriate dimensions, then these will produce air-borne sounds for long-range communication (Refer Figure 2.26).

This mechanism of producing sounds and vibrations is common for many insects such as Locust, bugs and beetles. Stridulatory organs have modifications of various exoskeletal structures and appendages of insect bodies including wings, legs, antennae, mouthparts and segmental joints.

Insects also use following methods of stridulation:

- Tegminal stridulation involves t*egmina* (singular Tegmen) which are thickened fore wings. It occurs in crickets (Refer Figure 2.26) and bush crickets.
- Femoro-tegminal stridulation occurs in grasshoppers.
- Sound production by abdomino-alary stridulation is present in mantids.

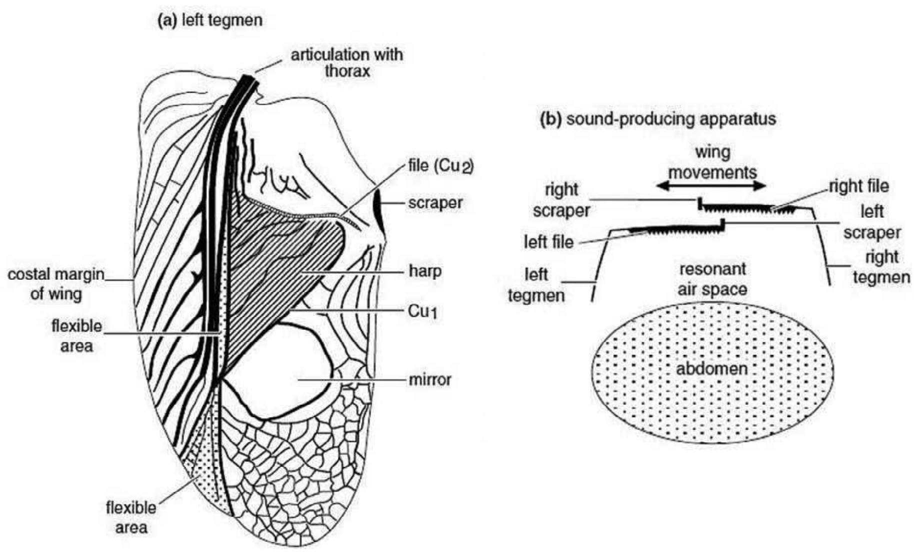

Fig. 2.26 *Stridulation in Crickets*

In above Figure 2.26 stridulation in crickets is shown in which A. shows left tegmen of cricket seen from above; and B. shows diagrammatic cross-section through an anterior abdominal segment of a stridulating cricket.

iv. Timbal or Click Mechanisms

A timbal also called tymbal is a region of thin cuticle bordered through a rigid frame. Vibrations are produced when the timbal buckles that means timbal becomes alternately distorted and relaxed by a muscle attached to inner surface of timbal. Timbals are present in cicadas, planthoppers, aphids and mealybugs and tiger moths.

Timbal Mechanism in Male Cicada

Structure: The timbal is an irregular region of thin cuticle. It is located dorso-laterally on each side of the first abdominal segment. It comprises of membrane made up of resilin held by a sclerotized rim. Membrane has a sequence of dorso-ventral sclerotized ribs. At posterior, it has heavily sclerotized region known as **timbal plate**. On the inside, a cuticular compression strut moves from the ventral body wall to the posterior edge of supporting rim. A timbal muscle runs parallel with compression strut and connects to an apodeme attached to timbal plate (Refer Figure 2.27A).

Mechanism: Contraction of timbal muscle causes timbal to buckle inwards. There is a tensor muscle that connects anterior rim of timbal with a knob on metathorax. Contraction of tensor muscle pulls rim of timbal so that curvature of rim is increased.

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Tension of tensor muscle controls resistance of timbal to buckling upon timbal muscle contraction. The timbal is backed by an air sac which surrounds the muscle and communicates with the outside via the metathoracic spiracle. The presence of the air sac leaves the timbal free to vibrate with a minimum of damping.

Sound is produced through in- and outward buckling of timbal membrane. Buckling might takes place in a single movement or in a sequence of graded movements as ribs give way. It is based on arrangement of vertical ribs on timbal and on tension applied by tensor muscle. Each constituent of buckling can create a pulse of sound. When muscle relaxes, timbal moves back to its original position by dorsal resilin pad (Refer Figure 2.27B).

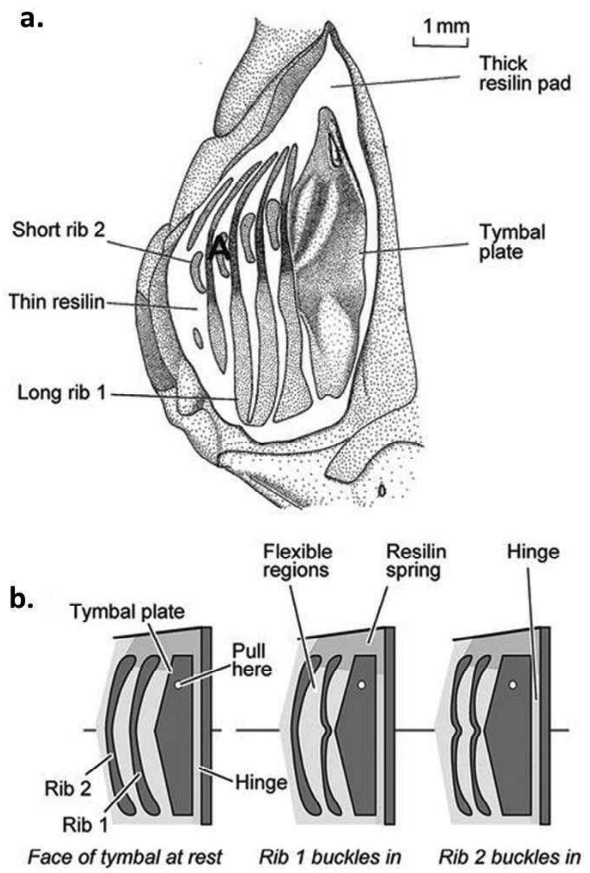

Fig. 2.27 *Timbal or Click Mechanism*

In above Figure 2.27 timbal (tymbal) or click mechanism is shown where A. shows a schematic diagrams of a single timbal organ exhibiting its various parts; and B. shows the method of excitation of sound resonances in the timbal organs. As the membrane's ribs buckle inward, clicks or sounds are created.

v. Flight Muscles

Oscillation of flight muscles creates thoracic and wing vibrations that are utilized in communication by several insects.

Sound Production by Flight Muscle in Honey Bee: Honey bees use their flight muscles to produce vibrations important in social communication. A worker bee returning from foraging performs a waggle dance during which air-borne vibrations are produced through the wings that are held horizontally above her back. These vibrations usually possess a frequency of 250–300 Hz, near to the wing beat frequency and are made in 30 second pulses.

They are perceived as near-field sounds, i.e., particle displacement through antennae of following workers. At the same time, these workers can produce stop signals (formerly called as begging calls). These are also formed by vibration of flight muscles. But these sounds are transmitted through legs of insects to hive's comb, which conveys the vibrations.

vi. Air Expulsion

Expulsion of air is a rare mechanism of sound production in insects. The death's head hawk moth repeatedly sucks in and expels air through mouth by dilating and contracting its pharynx. Through vibrations of the epipharynx the intake of air produces a series of sound pulses with maximum intensities at frequencies of 7–8 kHz. Subsequent contraction of pharynx with epipharynx held erect expels the air and thus produces a whistle.

2.5.3 Types of Songs and their Significance

Structure and Features of Song

Most insect songs cover frequency range of 2,000 Hz to 15,000 Hz and beyond. Followings are six primary terms or elements needed in describing insect songs:

- **Note:** It is composed of pulses, but these usually are too rapid to be discerned by ear, for example tree cricket songs.
- **Trill:** A trill is defined as a continuous train of notes or pulses given too fast to count and usually lasting several seconds or more. Pulses slow enough to be discerned, for example jumping bush cricket.
- **Chirp:** A chirp is a very short bundle of rapid and irregular notes (a very short trill lasting a fraction of a second). It is usually given in a series, with each chirp being followed by a brief period of silence, for example spring and fall field crickets.
- **Drone:** It is mechanical analog of a note, for example striped ground cricket.
- **Buzz:** It is mechanical analog of a trill and like a trill its length can be short (the elements of a common true katydid song), intermediate (as in most meadow katydids) or extended (as in rattler round-winged katydid).
- **Tick:** It is briefest of mechanical sounds. Examples are found in typical song of greater angle-wing and series of brief sounds leading into buzz in songs of meadow katydids.

Courtship songs have elements such as ticks, trill and chirps. For example, Crickets produce musical trills or chirps that fall on a definite pitch that is usually below 10,000 Hz. Cicada are known for their loud and penetrating songs. Most fall below 10,000 Hz and are variously described as rattling buzzes or harsh trills.

Each species has its own distinct song, which is recognized by all individuals of same species. Insects can create songs for different purposes such as calling songs, courtship songs, mixed courtship songs and aggression songs. Details about these songs are explained below:

i. Calling Song and Courtship Songs

In crickets and grasshoppers the calling song is used to attract a mate. It changes to courtship song as soon as both sexes establish visual contact. During courtship song, male try to grasp female for mating. The courtship song is of lower intensity (i.e., quieter) than the calling song. In many crickets, principal component of courtship song is also at a higher frequency than that of calling song (Refer Figure 2.28). In insects that do not produce calling songs for acoustic mate attraction, courtship songs serve as major cues for species recognition.

Calling and courtship songs are signals of reproductive readiness. These song types are usually generated by sexually mature males, but their production may be suppressed during post-copulatory periods. Stridulating females are highly attractive to grasshopper males, since they signal high reproductive motivation.

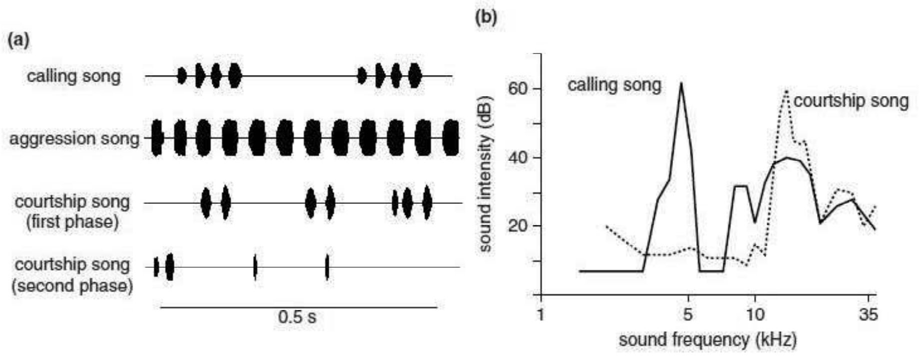

Fig. 2.28 *Acoustic Signals of Cricket*

The above Figure 2.28 illustrates Acoustic Signals of Cricket where; A. shows Patterns of Sounds Produced by Tegminal Stridulation by a Male Cricket in Different Situations and B. shows Frequency Spectra of Calling and Courtship Songs. The Sound Intensity of Calling Song is Maximum at about 4 kHz. The Highest Intensity of Courtship Song Occurs at Around 16 kHz.

Song Patterns during Courtship in Katydids and Crickets

- A large part of time, both day and night, males produce calling song (plate 1) (Refer Figure 2.29). This song attracts females, which move toward and locate males.
- When a singing male is approached by another male, he stops regular chirping of calling song and delivers one or louder, clearer and longer chirps (plate 2).
- While a male adult singing a calling song is approached by a female. This is loud and clear chirps having a large number of pulses (plate 3).
- These chirping results continuously into randomly recognized as pre-courtship singing (plate 4). When uninterrupted, it eventually converts into mixed courtship singing (plate 5 in) and full courtship singing (plate 6) (Refer Figure 2.30).
- Pre-courtship singing is produced from softer and less musical chirps than those created in the calling song.

- Mixed courtship singing having a combination of soft pulses created in full courtship with louder and clearer pulses similar to those of the calling song.
- Full courtship singing have a rhythmical repetition of several pulse chirps, each of which ends in a louder and clearer tick, exhibited in plate 6 through the slender vertical mark between pulse groups.
- Mixed courtship singing exhibits a stage between pre-courtship and full courtship events. It is continued for long periods of time when female is not fully stimulated by courtship behaviour of male.
- If a female leaves a courting male, or another male approaches while a male is courting, he delivers loud, clear, many-pulse type of chirp (plates 7, 8) which is also characteristic of male and female encounters.

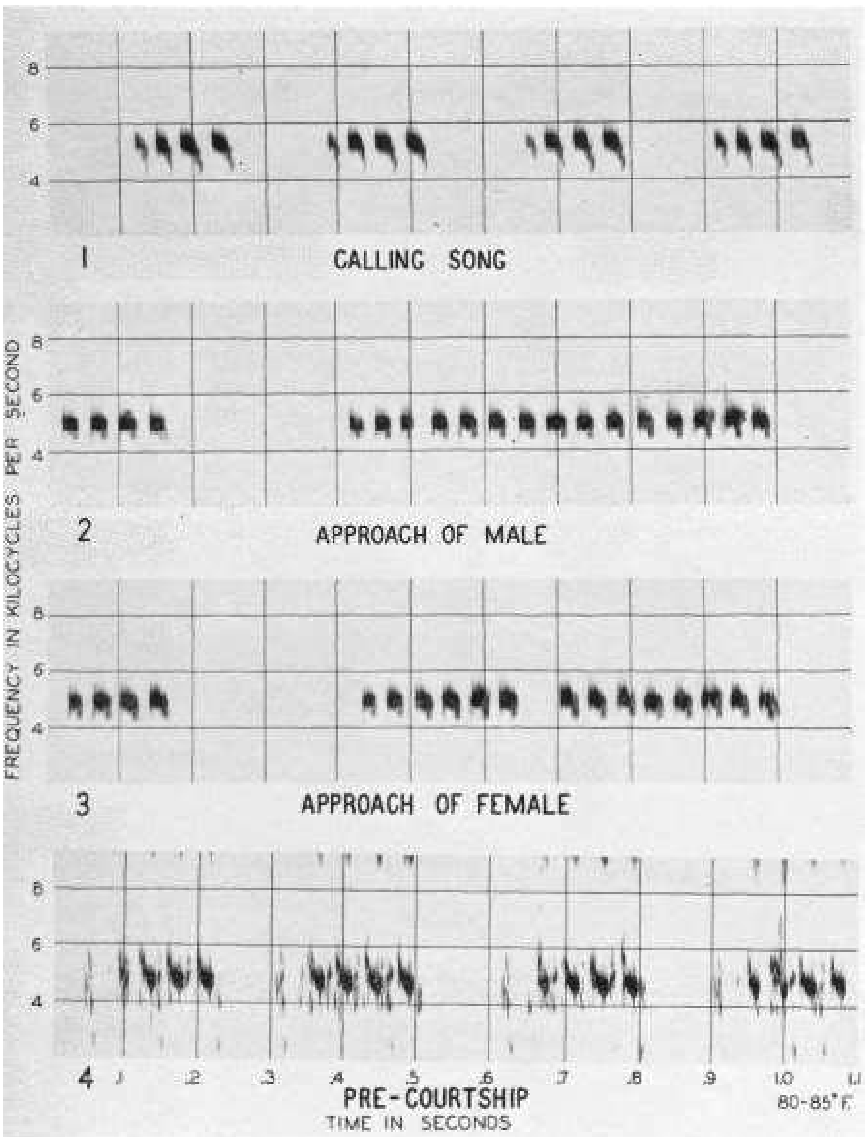

***Fig. 2.29** Vibragrams (Plate 1-4) of Sounds of Mountain Field Cricket for Illustration of Types of Songs for different Insect Activities*

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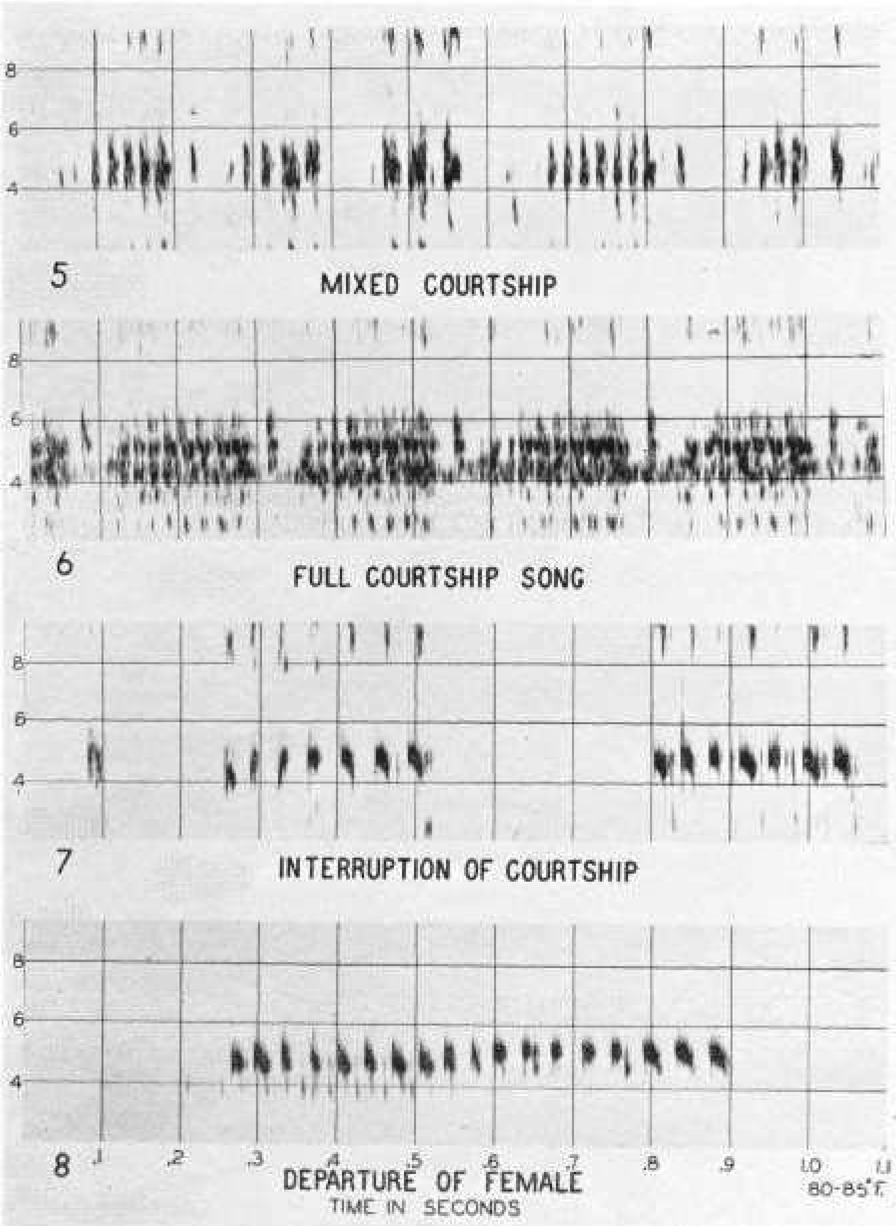

Fig.2.30 *Vibragrams (Plate 5-8) of Sounds of the Mountain Field Cricket for Illustration of Types of Songs for Different Insect Activities*

ii. Aggression Song

The calling song, when attracting females, at same time, can serve as an aggressive signal to other males (for example, whistling moths and grasshopper). But many insects have a separate aggression song. Long-range acoustic signals enable males to claim large territories without showing physical presence in all its areas. The territories may include burrows or high-quality food sites that may serve as additional cues for females to select a singing male for reproduction.

Aggressive stridulation observed in various territorial cricket species such as European field cricket, two-spotted cricket and common tree cricket. If a male intruder enters territory, both resident and intruder generate aggression songs. The subsequent agonistic interactions include threat displays, physical combat and occasional sequences of aggression song. Encounters are decided by the retreat of the loser, who finally leaves disputed territory, while the winner usually continues to present aggression song.

iii. Chorusing Songs

In some insects, calling song may serve to attract males to a group chorus whose combined sounds attract females to the area, for example cicadas. Sometimes sounds produced by male insects attract other males as well as females. Males may aggregate at preferred sites for feeding or oviposition and sing together (chorusing) during particular daily periods.

Significance of Songs

Song pattern of sounds and vibrations is used to attract reproductive partners from a distance, to create copulatory readiness during courtship, to defend territories or other valuable resources and to recruit conspecifics to a feeding site or to defend against intruders. Followings are the detailed significances of songs:

- **Attract Mates:** The great majority of insect songs that we hear in nature are calling songs of males, produced primarily to attract mates. Calling songs may have other functions as well.
- **Chorusing:** Chorusing occurs in bushcrickets, grasshoppers and cicadas. It enables direct comparison of several males during mate choice of the attracted females. Chorusing may increase the effective range of male calling signals, enhances female sexual responsiveness and reduces risk of predation. Alternatively, the mating song may function to keep males optimally dispersed within singing colonies, for example Meadow katydids, Coneheads, and Cicadas.
- **Courtship:** Courtship singing enables insects to accomplish mating and thereby spermatophore is transferred to female. Thus, courtship song is necessary for successful copulation. It can also shorten time between meeting of sexes and copulation.
- **Territorial Behaviour and Competition:** Some insects give aggressive sounds when two males encounter one another. Field crickets are a good example. Certain species may also respond with disturbance calls when handled. For example, Common true katydids give loud raspy calls when touched.

Sound Production in Different Insects

Sound production in insects like cockroach and honey bee is discussed below:

I. Cockroach

Cockroaches produce sounds during courtship and mating. They produce sounds by stridulation. In this, chirping sound is produced by male rubbing its pronotum (covers dorsal surface of thorax) against its costal veins. Cockroach also produces sounds where insect feels threatened. Typically, this occurs between two or more males, but just about any animal or insect can cause threat.

Cockroaches hisses by expelling air from a pair of specialized abdominal spiracles. This loud hiss contains information about the size of the roach producing it. When two male Madagascar hissing cockroaches approach and hear each other, the larger male's hiss lets the smaller male know who is in charge. This does not mean dispute would not occur, but it does give each cockroach an idea of what they are about to come up against.

II. Honey Bee

A variety of different sounds have been described in bees. Most of them are characterised by a low fundamental frequency (300 to 600 Hz) and its harmonics. Bees are not equipped with structures especially designed for the effective production of acoustic signals.

- Bees produce sounds by a kind of siren mechanism that is compressing air in air sacs and releasing it through the abdominal spiracles.
- In bees, which do not possess a stridulation apparatus, a harp or a tymbal, the sounds are generated by rhythmic thoracic oscillations.
- Sound made by young queens during the process of swarming is called as queen piping. Two different types of sounds are produced by bees during piping. Young queens emerging from cell in which she developed produces a sound signal called tooting. Other young queens, which are still sitting in their cells, respond by quacking sound.
- Vibrational signals are also found in worker communication. Bees attending the dances of their nestmates from time to time make short squeaking sounds. Squeaking sounds are airborn sounds, but transmitted as vibrations of comb. The signals (Refer Figure 2.31) typically last for = 100 ms (millisecond) at a frequency of =350 Hz and amplitudes of =1 μm comb displacement. The emitters press thorax against comb and by doing so induce substrate vibrations by contraction of wing muscles. The dancers then sometimes but not always stop dancing and deliver small samples of collected food to dance attenders. The signal therefore is called is begging signal.

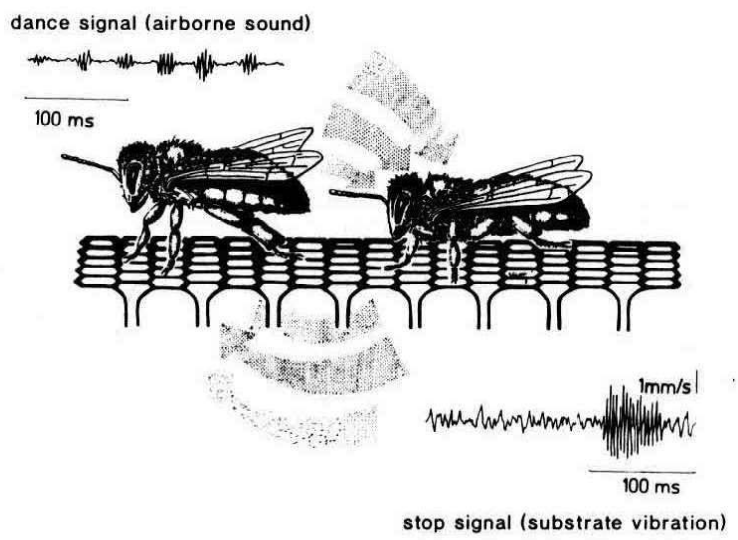

Fig. 2.31 *In Dance Language Dancing Forager Bees Emit Airborne Sound Signals by Dorso-Ventral Oscillations of Wings. Recruits Produce Substrate-Borne Vibrations, which Propagate Through Wax Comb*

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Check Your Progress

22. How do insects produce sound?
23. What is a pitch?
24. Give a difference between Oscillation and wavelength.
25. What are acoustic signals?
26. List the body parts of insects that are responsible in producing sound.
27. What is percussion?
28. Define the term stridulation.
29. What are the methods of stridulation used by insects?

2.6 MECHANORECEPTORS AND CHEMORECEPTORS

The environment is always changing so insect has to maintain itself to sense these changes. There are specialized structures (Refer Figure 2.32) which receive this information to central nervous system. Mechanoreceptors in insect can sense mechanical stimuli that are produced from touching an object or from vibrations borne through air, water or substratum. Insects have gustatory and olfactory chemoreceptors to detect different chemical elements in their environment.

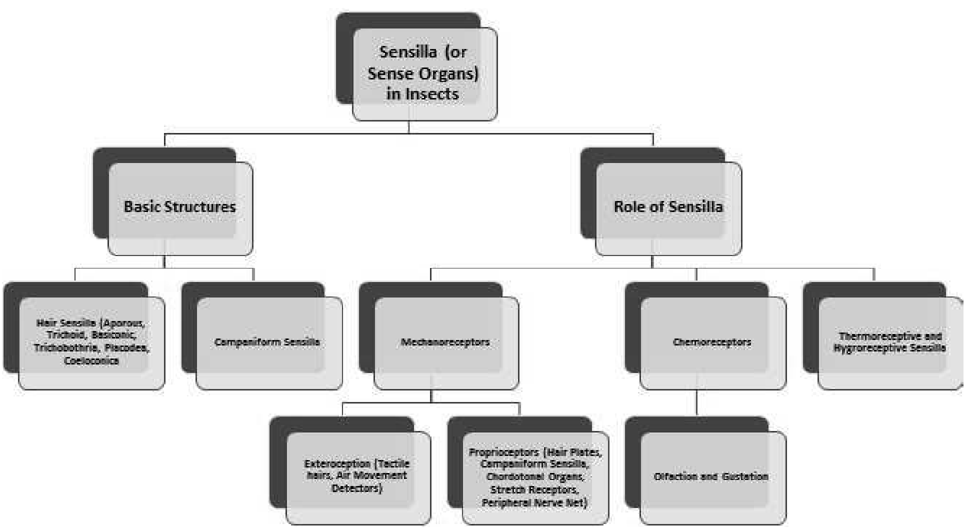

***Fig. 2.32** Sensilla or Sense Organs in Insects*

2.6.1 Basic Structures of Sensilla

Sensillum (plural sensilla) is an insect sensory organ protruding from cuticle of exoskeleton, or lying within or below it. Sensilla occur as small hairs or pegs over an individual's body. Inside each sensillum there are two to three sensory neurons. These neurons, or receptors, gather information about environment. These receptors are mechanoreceptors, chemoreceptors, thermoreceptors and hygroreceptors.

Sensilla are divided into two broad categories namely **hair-like structures** or **hair sensilla** and **campaniform sensilla**. These are discussed below as follows:

i. Hair-Like Structures or Hair Sensilla

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The wall of the hair composed of exocuticle with an outer layer of epicuticle. The hair-like structure arises from a socket allowing movement of hair. Neural stimulation takes place due to the dislocation of the hair in its socket. To provide flexibility and grip to the hair in its normal position, the socket has three components:

- A thin cuticular combined membrane is continuous with common body cuticle and that of hair.
- Under this, there are rings of suspension fibers to bridge a gap between body cuticle and hair.
- Finally, socket septum present on inside of socket. It occurs throughout the outer area of the receptor lymph cavity to the dendrite sheath (Refer Figure 2.33).

Various types of hair sensilla are based upon features of their cuticular parts. Following hair sensilla are necessary to understand as they have important role in mechanoreception, chemoreception and thermo-/hygroreception:

- **Aporous Sensilla**: In aporous sensilla there are no pores except molting pore, in the cuticle of hairs and perform specially as mechanoreceptors and thus these hairs are called as aporous sensilla.
- **Trichoid Sensilla**: When the hairs taper from base to tip, they are referred as trichoid sensilla. Several of these sensilla are sensitive to touch through deflection.
- **Basiconic:** These are shorter, peg-like appearance of chemosensory and mechanosensory hairs having only one pore at the tip.
- **Trichobothria:** Mechanosensory hairs on the cerci of insects such as crickets and cockroaches, are very long comparative to their diameter and do not taper and these are termed as trichobothria.
- **Placodea:** These sensilla are the chief olfactory sense cell. This olfactory receptor is a thin-walled plate with many pores through which airborne molecules diffuse. Odorant molecules, such as pheromones reach the dendrites of olfactory responsive neurons by diffusing through the extracellular fluid, i.e., the sensillum lymph.

  These olfactory receptors are most abundant on the antennae. These also present in the mouthparts or external genitalia.
- **Coeloconica:** This sensillum is modified from basiconic sensillum and has hygro-and thermoreceptive properties. The cuticular apparatus of this sensillum is a mushroom shaped protrusion set in a narrow cylindrical pit. This sensillum does not have pores, if occur it is at tip of the sensillum. These have three or four receptor cells.

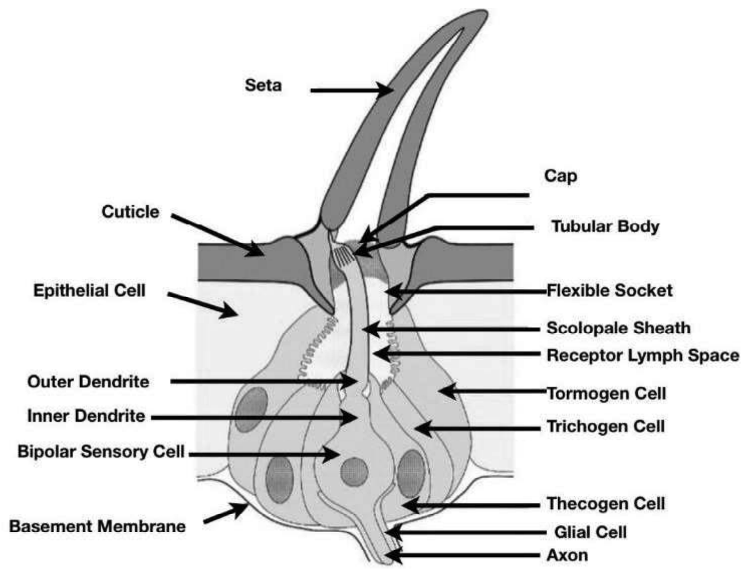

Fig. 2.33 *Diagrammatic Section of Mechanoreceptor Hair Sensillum (Trichoid Sensillum) in Bee*

ii. Campaniform Sensilla

Campaniform sensilla in insects are regions of thin cuticle and oval in shape. These sensilla have diameter in range of 5-30 mm and having domed on top. The dome of thin cuticle has an external homogeneous layer appearing like exocuticle and an internal lamellar or fibrous layer (Refer Figure 2.34). The dome is joined to the neighboring cuticle by a joint membrane. A single dendrite enclosed by dendrite sheath and in turn it is inserted into center of dome.

Campaniform sensilla are located in regions of the cuticle on the insect body parts that are exposed to stress. They occur most commonly on appendages and thus they are situated near to the joints. There is a single campaniform sensillum at the base of each of the tibial spines for instance in some orthopteroid insects, for example cockroaches. Large numbers of campaniform sensilla occur on the haltere of flies. An adult of bottle flies has about 1200 campaniform sensilla out of which about 36 present on each leg, 140 on each wing base and 340 on each haltere.

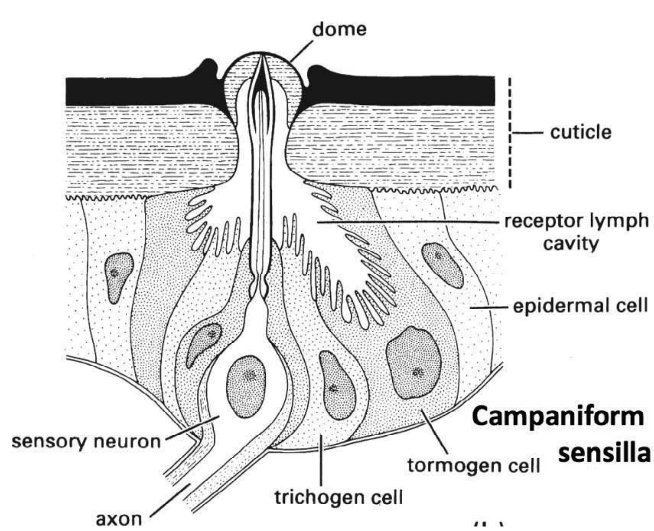

Fig. 2.34 *Diagrammatic Representation of Campaniform Sensillum on Haltere of a Fly*

2.6.2 Physiology of Various Types of Mechanoreceptors

Mechanical sensilla provide the insect with to make directed orientation, general movement, fight from enemies, reproduction and feeding. These are receptors which sense mechanical stimuli as they are sensitive to physical touch to solid surfaces, air movements, sound waves and gravitational forces. Even they can detect their position in air and water while flying and swimming.

Various Types of Mechanoreceptors

In all insects, some hair sensilla sense stimuli borne outside of insect body, i.e., from environment and referred exteroception, while others sense the insect's own movements and thus act as proprioceptors.

i. Exteroception

In exteroception, hair sensilla response to external stimuli. They are involved with the sense of touch (tactile), movement of the nearby air or water, or even with location in relation to gravity.

Tactile Hairs: Hairs responding to tactile stimulation are widely distributed over the insect's body, may be present in large numbers and may vary considerably in length. On the middle leg of Locust, for example, there are 1500–2000 mechanosensitive hairs. These hairs usually taper from the base and are generally curved and set at an angle to the surface of the cuticle.

Air Movement Detectors: Some insects have hairs that are specialized for the detection of air movements, sounds. Grasshoppers have groups of small trichoid mechanoreceptors on specific regions at front and top of head or on prothorax. These hairs are stimulated by flow of air over head and body when insect flies. They are responsible for maintenance of wingbeat, and are called aerodynamic sense organs.

ii. Proprioceptors (Position Mechanoreceptors)

Proprioceptors are sense organs that respond continuously to deformations (changes in length) and stresses (tensions and compressions) in insect body. They provide an insect with information on posture and position. Five types of proprioceptors occur in insects, i.e., hair plates, campaniform sensilla, chordotonal organs, stretch receptors, and nerve nets. Details of types of proprioceptors are explain below:

- **Hair Plates:** Groups or rows of small hairs occur at joints between leg segments, basal antennal segments, cervical sclerites, wing base. The hairs are positioned so that movements of one part of cuticle with respect to which may reflect different response properties and arranged in rows so that they are recruited in a graded way during a progressive movement of joint.
- **Campaniform Sensilla:** In the insect skeleton all stresses can be expressed as shearing stresses in the plane of the surface. Such stresses produce changes in the shape of the campaniform sensilla, resulting in their stimulation. They thus act as load sensors, and can respond to externally applied forces (loads) or to forces that result from the animal's own muscle activity.

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- **Chordotonal Organs:** These are specialized auditory organs and situated at joints in insects. They most commonly act as exteroception, for example sensing auditory stimuli and proprioceptors, for example leg movement.

Structure: They are made up of single groups of similar units called as **scolopidia**, which are attached to cuticle at one or both ends. Each scolopidium have three cells namely a sensory neuron, an enveloping or scolopale cell and an attachment or cap cell (Refer Figure 2.35). Scolopidia both directly or indirectly connect two joints and sense their movements relative to one another.

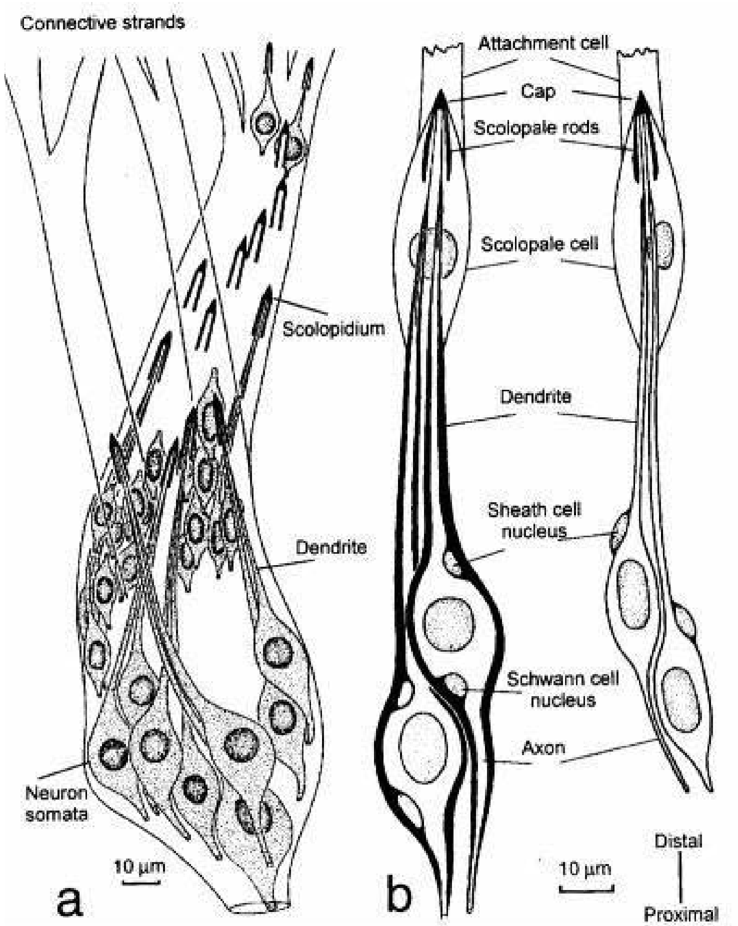

Fig. 2.35 *Chordotonal Organ on Cockroach Tarsus*

The above Figure 2.35 illustrates chordotonal organ on cockroach tarsus in which A. bipolar neurons with dendrites ending in scolopidia embedded in connective tissue; and B. shows morphology of two scolopidia.

Physiological Functioning: Chordotonal organs sense the stimuli by means of coupling mechanism. Through this mechanism external movement is transmitted to the dendrite of chordotonal organs. Thus, the movements of one cuticular plate relative to the other distort the scolopidium. Whatever the origin of the distortion, the effect is to displace the scolopale cap, producing sliding of the tubule doublets which leads to bending at the base of the cilium. The actin of the scolopale restores the position of the cap and dendrite after bending.

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Chordotonal organ that occurs almost universally in insects is Johnston's organ and some insects have also tympanal organs.

Johnston's Organ: It is situated in the antennal pedicel having its distal insertion in the articulation between the pedicel and flagellum. It is present in all adult insects but several larvae have its simplified form. It consists of a single mass or several clusters of scolopidia that sense movements of the flagellum with respect to the pedicel (Refer Figure 2.36). Johnston's organ can serve a variety of functions. For example, in bottle fly, Johnston's organ provide a measure of the degree of static deflection of third antennal segment as well as changes in its position.

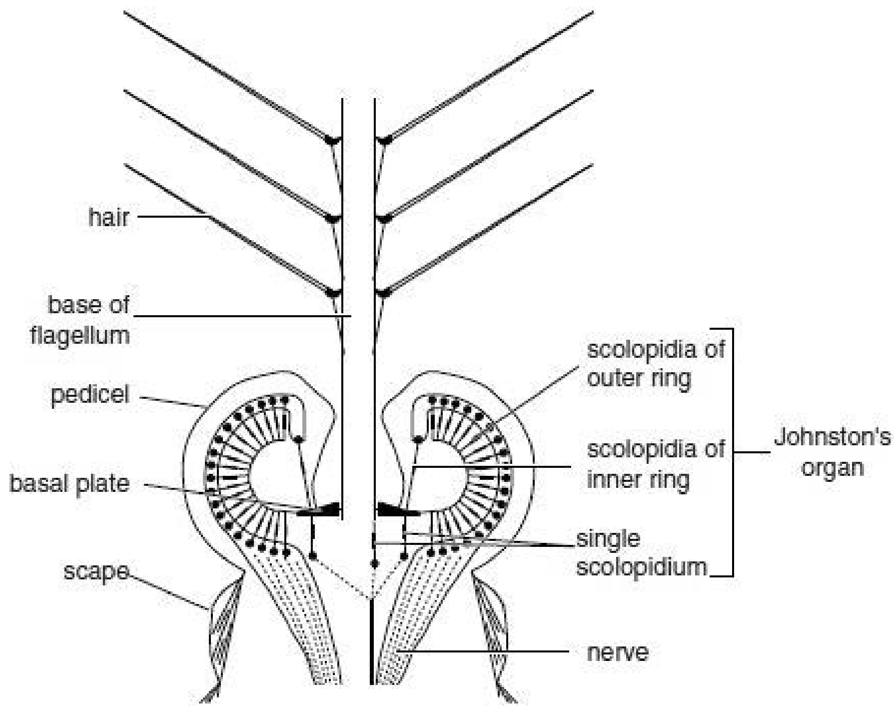

Fig. 2.36 Diagram Illustrating Structure of Johnston's Organ of Male Mosquito

Tympanal Organs: These are specialized for hearing. Tympanal organ has an area of thin cuticle, the tympanum also called tympanic membrane having air sac on its backside so that it can vibrate freely (Refer Figure 2.37). Chordotonal organ is attached to the inside or near tympanum. Number of scolopidium in this chordotonal organ varies from one (for example, Plea bug), to over 2000 (for example, some Cicada). Sound impinging on tympanic membrane causes it to vibrate. Aamplitude of vibrations varies with intensity of sound and structure of membrane. For example, different parts of the membrane in Locust, vibrate to some degree independently of each other.

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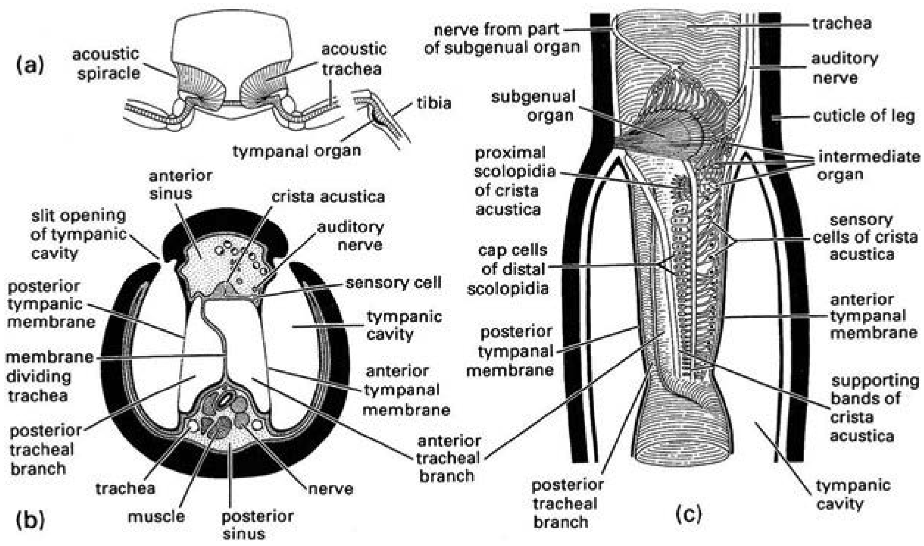

Fig. 2.37 *Tympanal Organs of a Katydid*

The above Figure 2.37 illustrates tympanal organs of a katydid where A. shows transverse section of forelegs and prothorax to show acoustic spiracles and tracheae; B. shows transverse section of fore tibia; and C. shows longitudinal view of fore tibia.

- **Stretch Receptors:** Stretch receptors attach to connective tissue and other end connected with body wall/ intersegmental membrane/ muscle and associated with multipolar neurons. It gives information the central nervous system about breathing movements, gut peristalsis and locomotion.
- **Peripheral Nerve Nets:** Nerve plexus/net consists of many bipolar and multipolar sensory neurons placed below body wall. It detects movement of joints and stress on body.

Physiology of Mechanoreceptor

Detection of stimuli by mechanoreceptors is a three-step process: coupling, transduction and encoding.

- **Coupling:** It is the deformation of sensory neuron's dendritic membrane caused by movement of hair in its socket, the inward movement of the cuticular dome in campaniform sensilla, or the stretching of the chordotonal sensillum.
- **Transduction:** It is the generation, followed by its flow through the dendritic membrane, of the receptor (generator) current. It results from the stretching of the membrane and the opening of transduction (stretch-activated) channels contained therein.
- **Encoding:** It is the final step that involves transfer of information from sensillum to central nervous system. This is a train of action potentials induced by the receptor current.

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2.6.3 Physiology of Various Types of Chemoreceptors

Chemoreception is a very important process in insects. It initiates some most important behaviour patterns of insects. For example, feeding behavior, selection of an oviposition site, host or mate location and behaviour integrating caste functions in social insects and responses to commercial attractants and repellents.

Various Types of Chemoreceptors

Chemoreceptors sense the smell (olfaction) and taste (gustation).

i. Olfaction

The cuticle of olfactory receptors has numerous small pores which allow entry of chemicals. These sensilla are known as multiparous (Refer Figure 2.38B). The pores are filled with an epicuticular lipid that coats the entire sensillum. Olfactory sensilla are mainly clustered on antennae, maxillary and labial palps. Olfactory sensilla also found on other body regions, for example the genitalia of some insects, for example the sheep blowfly.

ii. Contact Chemoreception

Contact chemoreceptor or gustatory sense organs in insects has only a single pore at the tip of a hair-shaped, i.e., trichoid sensillum, or a cone-shaped basiconic sensillum (Refer Figure 2.38A). All contact chemosensory sensilla are hollow inside. Contact chemosensory sensilla are present throughout the entire insect body, but occur most densely in specific regions. They are grouped on the mouthparts, where they occur on labrum, maxillae and labium. Sensory hairs and pegs occur both outside and inside the proboscis of moths and butterflies.

Structure of Chemosensory Sensilla: Process of olfaction and contact chemoreception is carried out by sense organs or sensilla called as chemosensilla. Chemosensilla are basically grouped in two categories namely thick-walled and thin-walled based on structural and functional criteria. These two groups broadly correlate with their functions as organs of taste and smell, respectively.

Thick-Walled (Uniporous) Chemosensilla: These are present in form of hairs, pegs or papillae (Refer Figure 2.38A). Generally, they serve as taste sensilla, but some are also sensitive to strong odours. Thick-walled chemosensory hairs have a rounded tip with a terminal pore, multineuronal innervation and dendrites that extend along length of hair to terminate just below pore. Papillae as chemosensory hairs present in the food canal of aphids, on the labellum of flies, and on the cockroach hypopharynx.

Thin-Walled (Multiporous) Chemosensilla: These are of various types (Refer Figure 2.38B) present on the antennae of all insects. They have a thin cuticular covering (0.1–1 ìm in width) perforated by many (up to several thousand) pores. Usually, below each pore is a small chamber from whose base numerous pore tubules connect with tonsillar sinus. Pores are filled with lipid that is transported to cuticular surface to reduce water loss. Most sensilla receive several neurons whose dendrites are much branched and terminate beneath the pore tubules. Thin-walled chemosensilla exist as surface hairs, pegs and plate organs (sensilla placodea).

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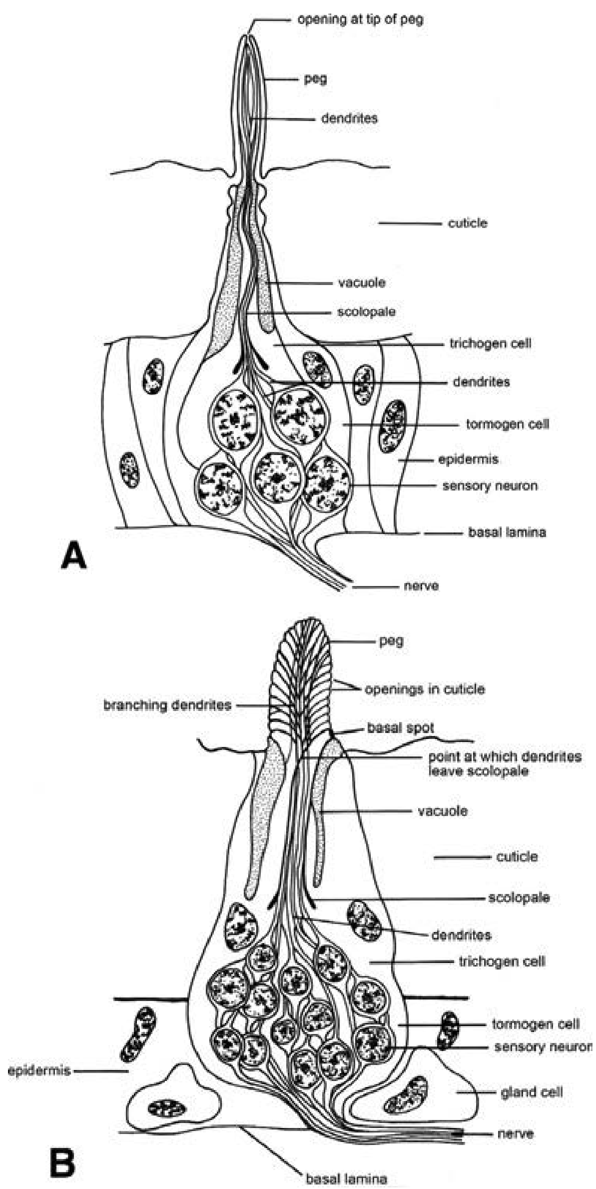

Fig. 2.38 *A. Thick-Walled Chemosensillum; and B. Thin-Walled Chemosensillum in Grasshopper*

Physiology of Chemoreception

Chemoreceptor stimulation involve processes namely, perireceptor activity, transduction and encoding.

- **Perireceptor Activity:** It is collection and transport of stimulants/deterrents to dendritic membrane of sensory neuron. At dendrite membrane, these chemicals couples with molecular receptors, leading to transduction.
- **Transduction**: In this process, the odorant or taste molecules induce changes in structure of membrane, leading to opening of ion channels, hence generation of receptor current.
- **Encoding:** It is transfer of stimulus from receptor to central nervous system by means of action potentials.

Perireceptor Activity in Olfaction: Odour molecules are generally lipophilic. On reaching sensillum, they dissolve in wax covering the pores. But they do not

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readily dissolve in the insect's body fluids. To reach dendritic membrane they must be solubilized in order to cross the fluid-filled sinus. This is achieved by attachment to Odorant-Binding Proteins (OBPs) or Pheromone-Binding Proteins (PBPs). On reaching dendritic membrane, odorant molecules are passed from OPBs to receptor proteins. This is an action that triggers via a second messenger system, the opening of ion channels and induction of the receptor current.

Perireceptor Activity in Gustation: Organic molecules in an insect's taste repertoire reach the dendritic membrane attached to binding proteins. On reaching the dendrites these molecules will bind to receptor sites to induce the receptor current. These seem likely to act directly on the ion channels to induce their opening and hence generation of the receptor current.

Tips of dendrites within single-pore sensilla are covered by a viscous fluid having mucopolysaccharides that exudes from terminal pore. This plug can be important in uptake of solids through terminal pore. In this way, the pore of contact chemoreceptors works in same way as pores in olfactory sensilla.

Thermoreceptive and Hygroreceptive Sensilla

Hygroreceptors exist as thin-walled, aporous hairs or pegs that are typically also thermo-sensitive. Each hygroreceptor contains dendrites of two neurons: dendrites that penetrate full length of hair are hygrosensitive, whereas those that terminate near base of hair are temperature sensitive (Refer Figure 2.39).

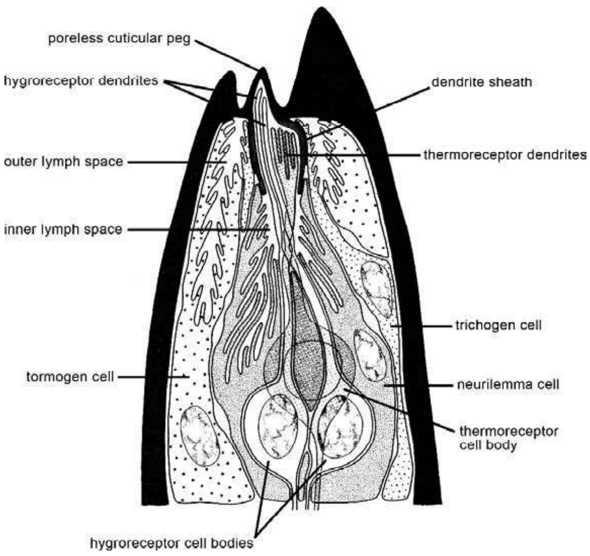

Fig. 2.39 *Thermoreceptive and Hygroreceptive Sensillum on Antenna of Silk Moth*

Sense Organs or Sensilla in Different Insects

Sense organs or sensilla in cockroach and honey bees is discussed below:

I. Cockroach

In cockroaches sense organs are scattered all over body, but are numerous on antennae, mouthparts, legs and wings. These sense organs (receptors or sensilla) are isolated or collective modifications of epidermal cells. A simple sensillum has a sensory cell connected with the fiber of a sensory nerve. Sensilla take different forms and have various functions.

- **Thigmoreceptors:** These are tactile hair sensitive to touch which are present on body surface, antennae, bristles of legs and maxillary palp. They help in searching food.
- **Chemoreceptors:** These are organs of taste and smell mainly confined to tips of maxillary, palps, labial palps, labium and hypopharynx.
- **Auditory Receptors:** Hair sensilla present on anal cerci respond to air or Earth-borne sound vibrations.

- **Propioreceptors:** Campaniform sensillae, present on the joints of maxillary palps and legs, perceive strains set up in cuticle during feeding and movement.

II. Honey Bees

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Main senses of the honey bee are smell, taste, touch, hearing, gravity perception, heat perception and time sense. Sense organs for these senses are given below:

- **Smell:** Majority of sense plates (sensilla placodea) on antenna of a bee varies with sex and caste of bee. On a single drone antenna there are about 500,000 sensilla, of which 30,000 are sense plates. Queen has 2,000-3,000 and worker has 5,000-6,000 sense plates. There can be up to 50 nerve cells within a single sense plate. Dendrites within the enclosing cell extend around edge of cavity formed by cap cell. The cuticle over cap cells is porous with some 2,400-3,000 pores. Lipoprotein traps the molecules over surface of plate and then molecules pass through pore tubules to surface of dendrite.
- **Taste:** Sensilla basiconica or peg organs are generally associated with taste. They exist at terminal 8 sub sections of flagellum (antennal part) and in mouth of bee. There are 3-5 nerve cells within organ and dendrites extend to apertures at end of peg.
- **Touch:** Sensilla for touch are found all over the body. There are 5 different types of trichoid sensilla ranging in form from short, slender, flexible to long, stiff, thick walled sensillae.
- **Hearing:** Sensilla scolopophora is associated with hearing. The organs differ from others in that they are elongated and the dendrites are embedded in two moveable parts that make them sensitive to vibration or movement. The subgenual organs are present on the legs of bee in groups. The Organ of Johnston on distal end of pedicel (antennal part) is a sensilla scolopophora.
- **Sense of Gravity:** Bee has hair plates at critical junctures of body: in neck region, at petiole and where legs meet thorax. Hair plates are groupings of mechanoreceptor sensilla. They act as proprioceptors which detect changes in the body. For example, head of bee hangs differently if it is facing up or down a comb. Therefore, hair plate can detect change and relate it to gravity.

Heat Perception: Sensilla coeloconica are peg like sensilla but the peg is sunk into a cavity. They are responsible for detecting carbon dioxide levels, temperature and relative humidity. There is more than one nerve cell per organ. The organs are in groups and are present at distal edge of flagellum.

Check Your Progress

30. What is the role of mechanoreceptors in insects?
31. How do insects detect different chemical elements in their environment?
32. Define the term sensillum.
33. In how many parts sensilla divided?
34. What are proprioceptors?
35. Name the types of proprioceptors found in insects.
36. What does coupling mean?

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2.7 MUSCLES IN INSECTS

Muscle is excitable and contractile tissue of animals which is responsible for body movement. Generally, muscles of insects are translucent and either colourless or grey, but the wing muscles usually are of yellow, orange or brown tinge. Unlike vertebrate muscles, fibers of both voluntary and involuntary muscles of insects are cross striated (Refer Figure 2.40).

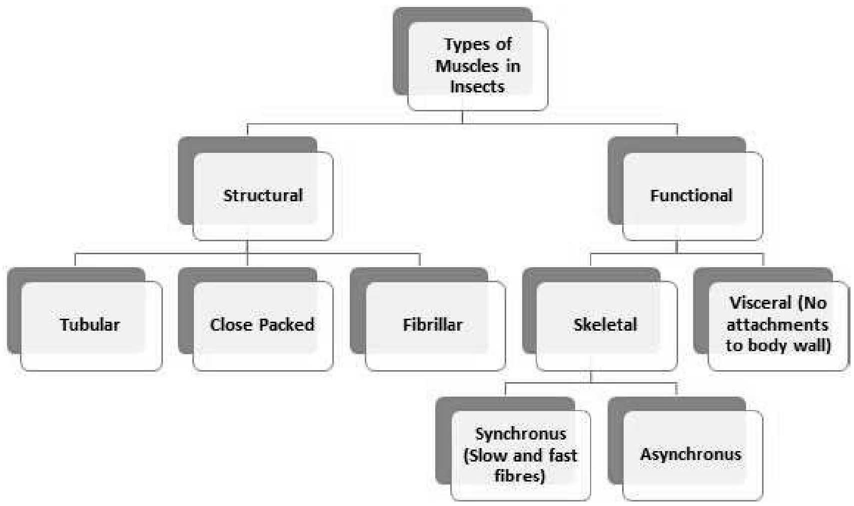

Fig 2.40 *Components and Types of Muscles in Insects*

2.7.1 Structure of Various Types of Muscles

Structure of various types of muscles is discussed below:

Basic Structure of Muscle

Each muscle is made up of varied number of fibers. Fibers are long and multinucleate cells running entire length of muscle. Generally, a muscle is arranged in units of 10–20 fibers. Each unit is separated from others by a tracheolated membrane. Each unit has a separate nerve supply.

Main components of a muscle fiber are explained below as follows (Refer Figure 2.41):

- The cytoplasm of fiber is called as **sarcoplasm**. Cytoplasm of fiber contains a varied number of mitochondria are referred as **sarcosomes**.
- Each fiber in muscle is bounded by sarcolemma that is plasma membrane of cell plus basal lamina.
- Endoplasmic reticulum has no connection to sarcolemma and is known as sarcoplasmic reticulum.
- Each fiber has a large number of myofibrils lying parallel in sarcoplasm and extending length of cell. Each myofibril contains contractile filaments which are made up of two proteins, actin and myosin. Thus myofibrils are long serial arrays of contractile units known as sarcomeres. Through their cyclical

ATP-dependent interactions, these proteins generate contractile forces and movements that shorten each sarcomere and the overall myofibril. In this way, proteins produce muscle contractions.

- In myofibril, thicker myosin filaments are surrounded by thinner actin filaments. Filaments of each myofibril within a cell tend to be aligned in such a manner that creates striated appearance (alternating light and dark bands) of the cell.
- The dark bands (A bands) correspond to regions where actin and myosin overlap, whereas the lighter bands indicate regions where there is only actin (I bands) or myosin (H bands).
- Each of the Z lines (discs) runs across fiber in center of the I bands, separating individual contractile unit called **sarcomeres**. Attached to each side of the Z line are the actin filaments, which in contracted muscle are connected to the myosin filaments by a means of cross bridges present at each end of the myosin.
- Plasma membrane (sarcolemma) is deeply invaginated into fiber, as regular radial canals between Z-discs and H-bands. This system of invaginations is called as transverse tubular or T-system.
- The T-system is associated with sarcoplasmic reticulum. Where the two membrane systems are very close, contacts between their membranes are visible as electron-dense material. This arrangement is called as dyad. Both T-tubules and dyads allow rapid transmission of electrical signals from sarcolemma to center of fiber. In this way, they cause release of calcium ions from sarcoplasmic reticulum and thus activate sarcomeric contraction.

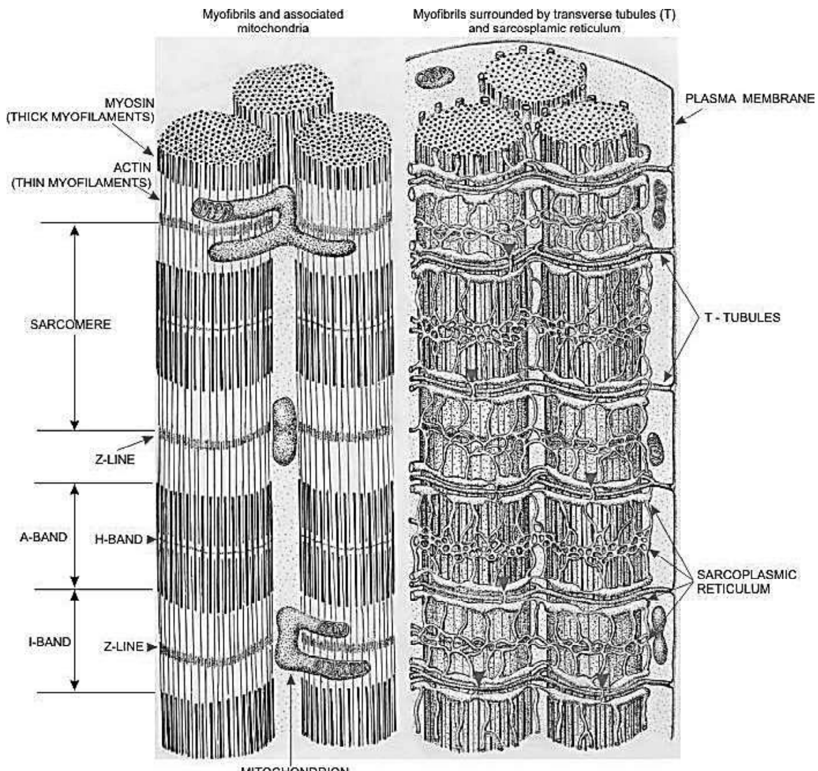

Fig.2.41 *Diagram of a Lateral View of Part of a Muscle Fiber Showing the Arrangement of the Major Components*

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Types of Muscles

Different types of muscles are classified on basis of following factors:

- Arrangement of myofibrils, mitochondria, and nuclei.
- Degree of separation of the myofibrils.
- Degree of development of sarcoplasmic reticulum.
- Number of actins surrounding each myosin.

These include tubular (lamellar), close-packed, and fibrillar muscles (Refer Figure 2. 42), all of which are skeletal and visceral muscles. Details of these muscles are explain below:

i. Tubular (Lamellar), Close-Packed and Fibrillar Muscles

- **Tubular (Lamellar):** Leg and segmental muscles of many adult insects and flight muscles of primitive fliers, for example dragonflies and cockroaches, are of tubular type, in which flattened (lamellate) myofibrils are arranged radially around central sarcoplasm. The nuclei are distributed within the core of sarcoplasm and the slab like mitochondria are interspersed between myofibrils.
- **Close-Packed:** Body musculature of wing-less and some larval winged insects, the leg muscles of some adult winged insects and flight muscles of Locusts and Butterflies are of close- packed type. In this muscle, myofibrils and mitochondria are concentrated in center of fiber and nuclei are arranged peripherally. In close-packed flight muscles, fibers are considerably larger than those of tubular flight muscles.
- **Fibrillar:** In most insects, the indirect muscles provide the power for flight. These are nearly always fibrillar muscle. In this type of muscle, individual fibrils are very large and together with massive mitochondria occupy almost all of volume of fiber. Very little sarcoplasm is present and nuclei are squeezed randomly between fibrils.

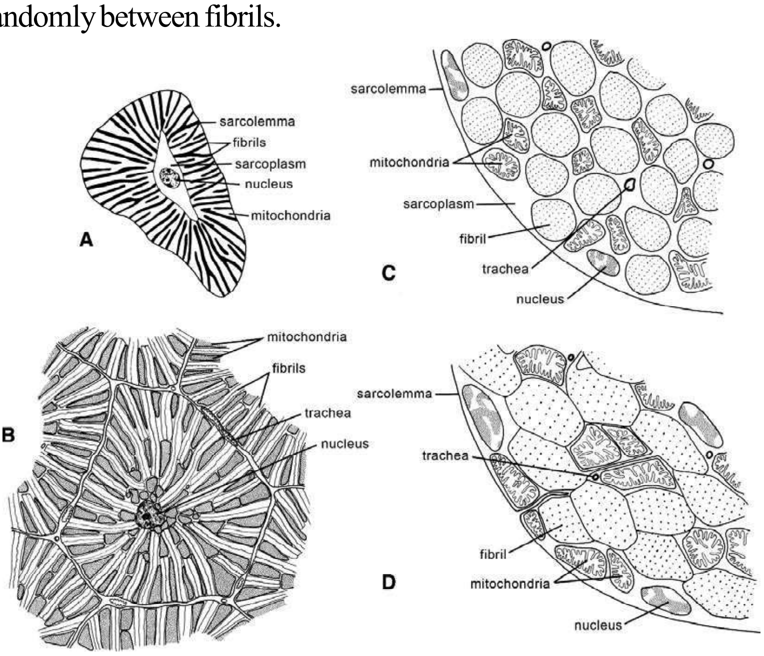

Fig. 2.42 *Transverse Sections of Insect Skeletal Muscles*

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The above Figure 2.42 illustrates transverse sections of insect skeletal muscles in which A. shows tubular leg muscle of wasp, B. shows tubular flight muscle of dragonfly, C. shows close-packed flight muscle of a butterfly; and D. shows fibrillar flight muscle of beetle.

ii. Skeletal and Visceral Muscles

Skeletal Muscles: Skeletal muscles are attached at either end to cuticle and move one part of skeleton relative to another. Skeletal muscles can be functionally divided into synchronous and asynchronous muscles.

- **Synchronous Skeletal Muscles:** Synchronous skeletal muscles have direct relationship between contraction and motor neuron activity. In this muscle each contraction is driven by a single neural stimulus. Majority of insect muscles are synchronous skeletal muscles.

The form and arrangement of myofibrils in synchronous skeletal muscles is quite variable. Tubular muscles have myofibrils arranged radially around a central core of cytoplasm containing nuclei. This arrangement is common in leg and trunk muscles of many insects. It also occurs in the flight muscles of dragonflies, Cockroaches and termites.

In synchronous muscles, invaginations of T-system occur midway between Z-disc and center of sarcomere. Sarcomere length in many synchronous muscles ranges from about 3 mm to 9 mm. But in flight muscles, it is usually about 3-4 mm. The I-band generally has 30–50% of resting length of sarcomere.

Slow and Fast Fibers: Synchronous skeletal muscles form a continuum with slow or tonic fibers and fast fibers. Features of slow and fast fibers are given in Table 2.3 below:

Table 2.3 *Slow and Fast Fibers*

S.No.	Slow Fibers	Fast Fibers
1.	Slow fibers contain minute sarcoplasmic reticulum.	Fast fibers have large sarcoplasmic reticulum.
2.	Large volume of cell is occupied by mitochondria.	It has a small volume of mitochondria.
3.	Ratio of thin to thick filaments is high (6:1).	It has low ratios (3:1) of thin to thick filaments.
4.	The sarcomeres are long.	It has short sarcomeres.
5.	Example is body wall muscle.	Example is flight muscle.

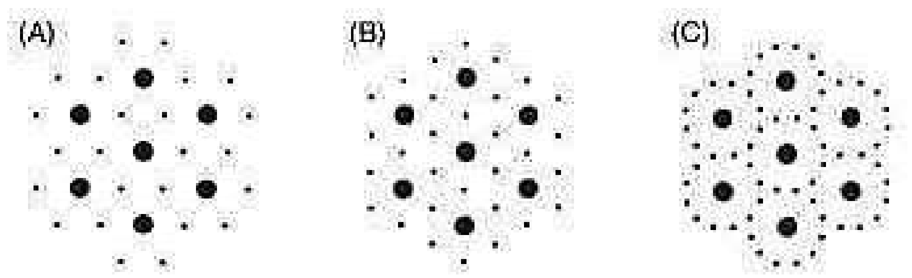

Fig. 2.43 *Organization of Thick and Thin Filaments as Seen in Cross Sections of Fibers from A. a Vertebrate Skeletal Muscle; B. a Fast Insect Muscle; and C. a Slow Insect Muscle*

- **Asynchronous Skeletal Muscles:** Asynchronous muscles do not have direct relationship between contraction and motor neuron activity. These occur in flight muscles of bugs, aphids, bees, beetles, flies and timbal muscles of some cicadas.

Asynchronous muscles have large cylindrical myofibrils, 1-5 μm in diameter, with fiber diameters, ranging from 30 μm in carabid beetles to 1.8mm in Rutilia flies. The myofibrils are large and easily separated. Muscles with such myofibrils are called fibrillar, but not all fibrillar muscles are asynchronous. Myofibrils are distributed through the entire cross-section of muscle fiber. Nuclei are scattered between myofibrils and under sarcolemma.

Plasma membrane is invaginated in T-system but positions of invaginations are variable. Regular reticulate patterns of T-tubule associated with sarcomeric structure. In wasp, they are aligned with H-band and in fruit flies where they lie midway between M- and Z-lines.

Mitochondria are large as in all flight muscles and occupy 30-40% of fiber volume. Almost the whole surface of each myofibril can be in direct contact with mitochondria. These may be regularly arranged, as between the Z-discs and H-bands in wasp, or without any regular arrangement, as in fruit flies.

Visceral Muscles

Visceral muscles move the viscera and have only one or no attachment to body wall. Many form circular muscles around gut, ducts of reproductive system and heart. Visceral muscles differ in structure from skeletal muscles in several respects. Followings are the features of visceral muscles:

- Adjacent fibers are held together by desmosomes which are absent from skeletal muscle, and in some cases the fibers may branch and anastomose, such as occurs in the Drosophila ovarian sheath.
- Further, each fiber is uninucleate and contractile material is not grouped into fibrils but packs whole fiber.
- As in other muscles, each fiber has thick and thin filaments in irregular matrix. Sometime it has rings of 10–12 Actin filaments around each Myosin filament.
- T-system with a regular arrangement is present in cockroach but in stick insect and flour moth it is irregularly disposed.
- Sarcoplasmic reticulum is poorly developed and mitochondria are small and few in number.

Muscle Insertion

Attachment of a muscle to the integument takes place when remains of the old cuticle are shed periodically. Thus, an insertion is able to break and re-form easily. A muscle terminates at basal lamina lying below epidermis (Refer Figure 2.44). The muscle cells and epidermal cells interdigitate, increasing surface area for attachment by about 10 times. Desmosomes occur at intervals and replacing the basal lamina. Attachment of a muscle cell to rigid cuticle is done through large numbers of parallel microtubules. Distally, the epidermal cell membrane is invaginated, forming numbers of conical hemidesmosomes on which microtubules terminate. Running distad from each hemidesmosome is one, rarely two, muscle attachment fibers.

Each fiber passes along a pore canal to cuticulin envelope of epicuticle to which they are attached by special cement. As cuticulin layer is first one formed during production of a new cuticle, attachment of newly formed fibers can readily occur. Until the actual moult, these are continuous with the old fibers and thus, normal muscle contraction can occur.

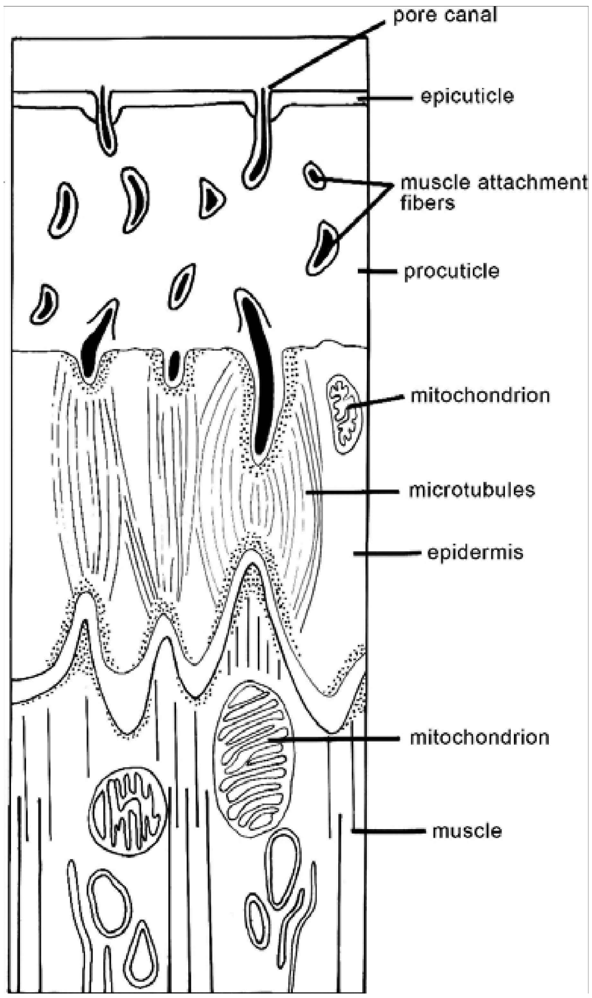

Fig. 2.44 *Attachment of a Muscle Fiber to the Integument*

2.7.2 Physiology of Muscles

Physiologic function of muscles involves following steps:

i. Muscle Contraction

As in vertebrates, insect muscles contract based on sliding filament theory. Arrival of an excitatory nerve impulse at a neuromuscular junction causes depolarization of nearby sarcolemma. A wave of depolarization spreads over fiber and into cell interior via T system. Depolarization of T system membranes creates a momentary increase in permeability of nearby sarcoplasmic reticulum. Thus, calcium ions stored in vesicles of reticulum, are released into sarcoplasm surrounding myofibrils. Calcium ions activate cross-bridge formation between actin and myosin. This enables filaments to slide over each other so that distance between nearby Z lines is decreased. Net effect is for muscle to contract (Refer Figure 2.45).

ii. Relaxation of Muscle

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Extension (relaxation) of a muscle results from opposing elasticity of cuticle to which muscle is attached. Commonly, muscles occur in pairs and each member of pair works antagonistically to the other. In this way, one muscle is stimulated to contract and its partner (unstimulated) is stretched. Previously unstimulated muscle is stimulated to begin contraction while active contraction of the partner is still occurring (cocontraction). This reduces contraction, thereby preventing damage to a vigorously contracting muscle. Also, in slow movements, it provides an insect with a means of precisely controlling such movements.

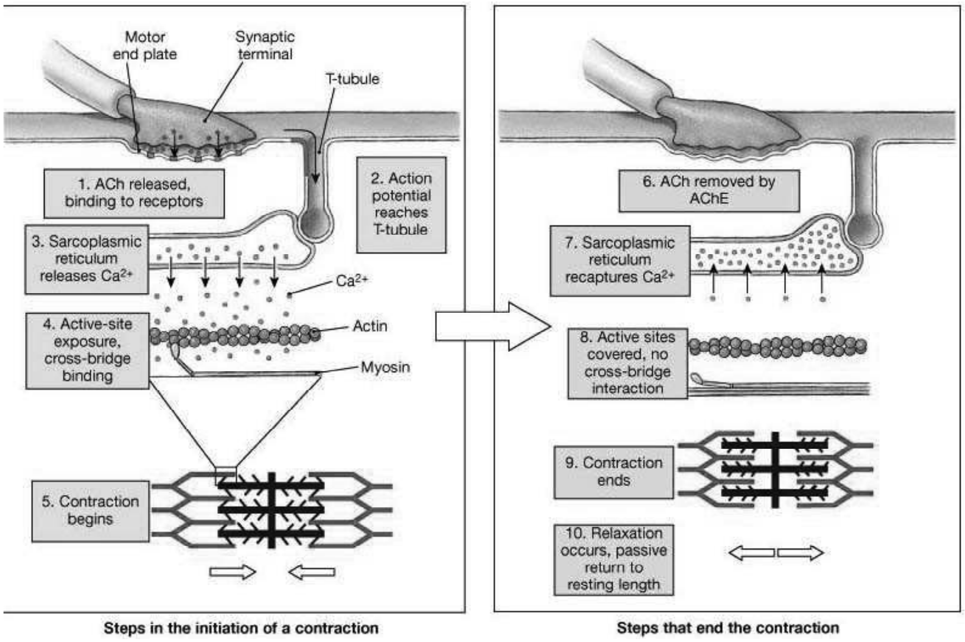

Fig. 2.45 *Steps in Initiation and End of Muscle Contraction*

iii. Excitation of Muscle

Activation of Muscle Fiber: Muscles are stimulated to contract by arrival of an action potential at neuromuscular junctions. For skeletal muscles L-glutamate is the usual chemical transmitter across the synaptic gap. For visceral muscles, L-glutamate and L-aspartate are chemical transmitters at neuromuscular junctions.

Fast and Slow Axons: Size of the muscle twitch (contraction) produced by excitatory action potential depends on whether stimulation occurs via fast or slow axons. Stimulation via the fast axon is occur to release a large amount of neurotransmitter and produces a large postsynaptic potential followed by a brief, powerful contraction of muscle. A single action potential from the slow axon releases a small amount of neurotransmitter and produces only a small postsynaptic potential followed by a very small twitch (muscle contraction).

Activation of Contractile System: A cycle of muscle contraction and relaxation is associated with calcium release and then its sequestration. Rapid removal of calcium from the system is associated with well-developed sarcoplasmic reticulum.

In general, twitch duration is inversely correlated with quantity of sarcoplasmic reticulum present.

Inhibition of Muscle Contraction: Some fibers of some muscles are innervated by inhibitory neurons. At an inhibitory nerve-muscle junction, a neural transmitter called ã-Aminobutyric Acid (GABA) is released. It causes a change in permeability at the postsynaptic membrane. It results in an influx of chloride ions. As a result, membrane potential becomes even more negative, the membrane is hyperpolarized and fiber tension decreases.

Muscular Control in Locomotion

Most behavioural activities result from coordinated activity of muscles. This is most evident in locomotion, which involves oscillation of an appendage such as leg or wing. For example, during slow walking by a cockroach, only slow axon to coxal depressor muscles is active. The strength and speed of contraction depends on the frequency of nerve firing. At walking speeds of more than ten cycles per second, the slow axon is supported by activity of fast axon, which also activates muscles. Inhibitory axons fire at the end of contraction and so ensure complete and rapid relaxation as antagonistic muscle contracts.

Muscles of Different Insects

I. Cockroach

Muscles are well developed and striated which provide quick movements to the body parts. The head and legs of cockroach are well muscularised, while abdomen is not so. The muscles are arranged in bundles.

The muscles are attached to inner surface of chitinous skeleton. The muscles of the legs, wings and jaws are very characteristic which provide an efficient movement mechanism to these parts.

The pink muscles of the coxa have a thin: thick filament ratio of 3:1 compared with a ratio of 6:1 in most of the other leg muscles. Sarcomere lengths are uniform in some muscles and variable in others. Fibres with reduced sarcoplasmic reticulum and an unusual T-system occur in coxal muscle.

II. Honeybee

Within the honeybee thorax there are two main types of muscles that directly or indirectly move the wings. Direct muscles are attached to all the wings; four to each forewing, three to each hind wing.

Axilla is the point at which thoracic *muscles* attach to wing of an *insect.* Muscles attached to the Axillary's causes control movements on the wings:

- AX1, controls figure of 8 wing tip pattern.
- AX2, enables the wings to be twisted to correct yaw, roll and pitch.
- AX3, used for furling and un-furling forewing below hindwing.
- AX4, assists AX3.

Hindwing has AX1-3 and a similar muscle structure.

Main role during flight is played by indirect muscles (Refer Figure 2.46). Chest cavity of a honey bee is entirely filled with them. The force in wings is provided by 2 pairs of indirect muscles namely dorso-ventral and longitudinal muscles.

The contraction of the longitudinal muscles and the relaxation of the vertical muscles extends the thorax vertically and drives the wings downward. In contrast, the relaxation of longitudinal muscles and contraction of vertical muscles bows thorax outward, driving the wings upward.

Flight speed and distance depends on the powerful thoracic muscles being amply supplied with energy derived from nectar metabolism; if the blood sugar falls below 1% the bee can no longer fly.

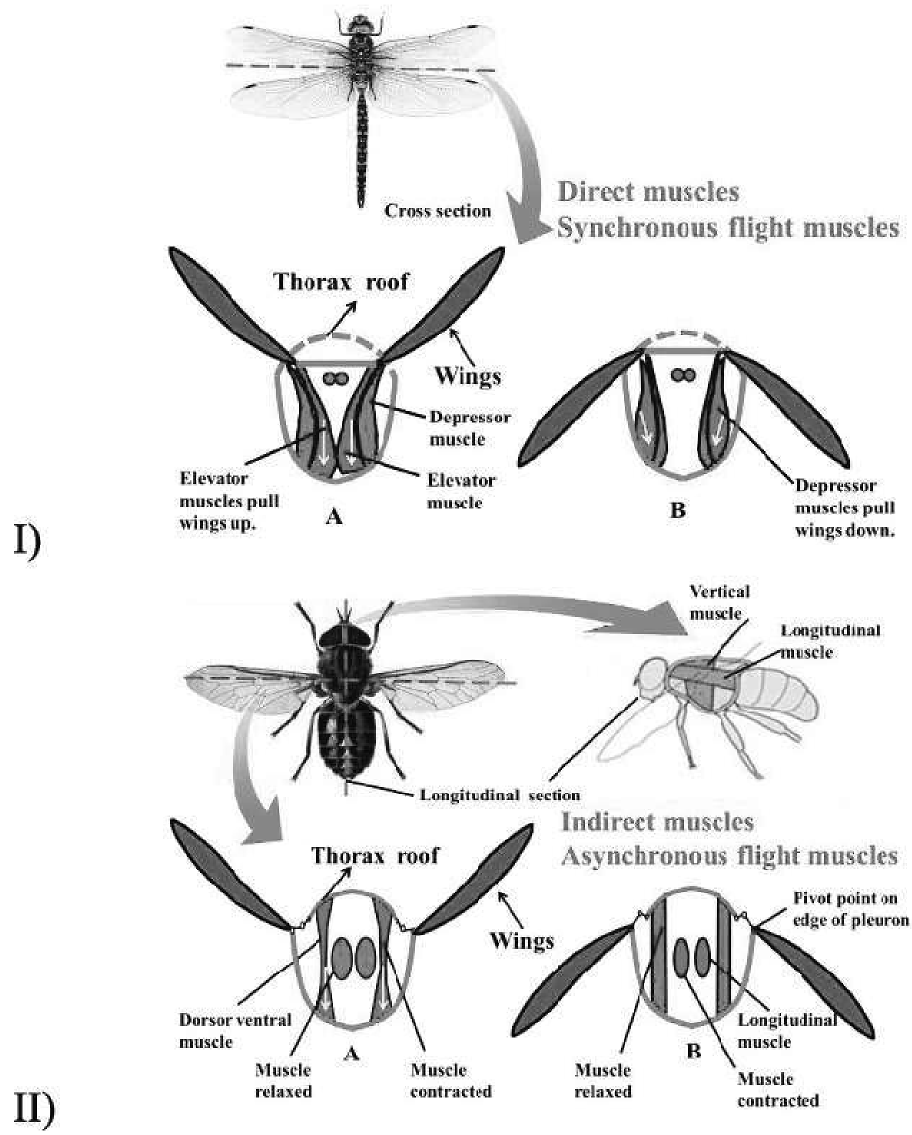

Fig. 2.46 *Thorax Mechanisms of Indirect Muscles*

In above Figure 2.46 thorax mechanisms of indirect muscles is shown, where A. shows how wings are stroked up by contracting vertical muscles pulling roof down; and B. shows contraction of longitudinal muscles between anterior and posterior ends of a thorax, and elevating up the roof, the wing is stroked down.

NOTES

Check Your Progress

37. What is a muscle?
38. What is the colour of muscles in insects?
39. How is muscle made of in insects?
40. How are skeletal muscles attached?
41. How does attachment of a muscle to the integument occurs?

2.8 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Regulation and synchronization of insect development is controlled by neuroendocrine system.
2. Endocrine glands are ductless glands or secretory organs of endocrine system that secrete their products, hormones, directly into circulatory system.
3. There are two kinds of endocrine organs in insects: i. specialized endocrine glands; and ii. neurosecretory cells, most of which are within the central nervous system.
4. The prothoracic gland is stimulated by brain hormone to produce another hormone known as moulting hormone.
5. Corpora Allata (CA) synthesize one of most essential hormones for insect development known as Juvenile Hormone (JH).
6. Neurosecretory cells are present in ganglia of central nervous system. They usually look like monopolar nerve cells. They typically secrete their products into haemolymph.
7. Products of medial Neurosecretory Cells (mNSC) are as follows:
   - o Prothoracicotropic Hormone (PTTH), which activates molt glands.
   - o Allatotropic and allatostatic hormones, whose primary function is to regulate the activity of the corpora allata.
   - o Diuretic hormone, which affects osmoregulation.
   - o Ovarian Ecdysiotropic Hormone (OEH) (formerly egg development neurosecretory hormone).
   - o Ovulation- or oviposition-inducing hormone.
   - o Testis Ecdysiotropin (TE).
8. The **nervous system** is a part of animal's body that coordinates its behaviour and transmits signals between different body areas.
9. The nervous system have two main types of specialized cells namely neurons and glial cells.
10. Neurons transmit signals between cells and from one part of the body to another. Glial cells regulate homeostasis and provide structural and metabolic support to neurons.

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11. Cell body of neuron is called as soma or perikaryon or neurocyte. Cell body has nucleus, many mitochondria, Golgi complexes and Rough Endoplasmic Reticulum (RER). Cell body plays major role in protein synthesis.
12. When an axon reaches a target, it terminates into multiple endings known as axon terminals (terminal arborization). The axon terminal is meant to convert electrical signal into a chemical signal in a process called synaptic transmission. Both axon and the collateral end in terminal arborizations of fine branching fibrils.
13. Space or gap between arborisations and dendrites is called as synaptic cleft or gap.
14. Endopterygote insects, also known as holometabola, develop wings inside body and undergo an elaborate metamorphosis involving a pupal stage. This is called as holometabolism or complete metamorphism.
15. In each visual organ, there are two functionally distinct parts namely, a dioptric apparatus and a receptive apparatus.
16. Dioptric apparatus transmits and condenses impinging light rays upon receptive surface. It always includes cuticle in the form of lens, largely formed by specialized cells of optic epidermis.
17. Receptive apparatus consists of sensory cells forming retina, which present specialized receptive surfaces at points where light rays are focused and are continued directly into optic nerve.
18. There are basically two kinds of eyes namely simple and compound eyes.
19. A simple eye or ocellus, is a photoreceptor having a single dioptric apparatus for all sense cells. A compound eye has numerous groups of sense cells and a separate dioptric apparatus for each group.
20. The dorsal ocelli (singular ocellus) are simple eyes of adult insects in addition to compound eyes and of exopterygote larvae and nymphs. Typically there are three ocelli: one median, located on upper part of frons or the frontal area of head and other two located more lateral on postfrontal region. Thus, they appear in a triangle. The dorsal ocelli are innervated from ocellar lobes which are positioned in protocerebrum, between mushroom bodies.
21. In eucone eyes each ommatidium contains a true crystalline cone, which is a hard refractive body formed as an intracellular product of cone cells. Examples of eucone eyes are locust, dragonflies, butterflies, bees and some bugs. Whereas, in pseudocone eyes type of eye, there is no true crystalline cone and the four cone cells are filled with a transparent, semiliquid material. Examples of pseudocone eyes are Muscoid flies, short-horned flies.
22. Insects produce sound either by rubbing one part of body to another part or one part by other external object.
23. Pitch refers to the quality that enables us to judge sounds as being higher and lower. A high-pitched sound causes molecules to rapidly oscillate, while a low-pitched sound causes slower oscillation.

24. Oscillation is the movement back and forth in a regular rhythm. Whereas, wavelength is distance that wave travels before it repeats itself. Wavelength itself is a longitudinal wave that shows compressions and rarefactions of sound wave.
25. Acoustic signals are noises (vibration, sound, etc.) that animals produce in response to a specific stimulus or situation, and that have a specific meaning.
26. Insect body parts and organs that are responsible for producing sounds are Head part, thoratic parts, legs and wings and abdomen
27. Percussion refers to vibrations produced by effect of body part against substrate or by clapping two parts of body against each other.
28. Stridulation refers to production of vibrations by moving a cuticular ridge on one body part over a toothed ridge on another.
29. Insects use following methods of stridulation:
    - Tegminal stridulation involves t*egmina* (singular Tegmen) which are thickened fore wings. It occurs in crickets and bush crickets.
    - Femoro-tegminal stridulation occurs in grasshoppers.
    - Sound production by abdomino-alary stridulation is present in mantids.
30. Mechanoreceptors in insect can sense mechanical stimuli that are produced from touching an object or from vibrations borne through air, water or substratum.
31. Insects have gustatory and olfactory chemoreceptors to detect different chemical elements in their environment.
32. Sensillum (plural sensilla) is an insect sensory organ protruding from cuticle of exoskeleton, or lying within or below it.
33. Sensilla are divided into two broad categories namely hair-like structures or hair sensilla and campaniform sensilla.
34. Proprioceptors are sense organs that respond continuously to deformations (changes in length) and stresses (tensions and compressions) in insect body. They provide an insect with information on posture and position.
35. Five types of proprioceptors occur in insects, i.e., hair plates, campaniform sensilla, chordotonal organs, stretch receptors, and nerve nets.
36. Coupling is the deformation of sensory neuron's dendritic membrane caused by movement of hair in its socket, the inward movement of the cuticular dome in campaniform sensilla, or the stretching of the chordotonal sensillum.
37. Muscle is excitable and contractile tissue of animals which is responsible for body movement.
38. Generally, muscles of insects are translucent and either colourless or grey, but the wing muscles usually are of yellow, orange or brown tinge.
39. Each muscle is made up of varied number of fibers. Fibers are long and multinucleate cells running entire length of muscle. Generally, a muscle is arranged in units of 10–20 fibers. Each unit is separated from others by a tracheolated membrane. Each unit has a separate nerve supply.

40. Skeletal muscles are attached at either end to cuticle and move one part of skeleton relative to another. Skeletal muscles can be functionally divided into synchronous and asynchronous muscles.
41. Attachment of a muscle to the integument takes place when remains of the old cuticle are shed periodically. Thus, an insertion is able to break and re-form easily.

2.9 SUMMARY

- Regulation and synchronization of insect development is controlled by neuroendocrine system.
- The neuroendocrine system comprises of nervous system and endocrine glands.
- There are two kinds of endocrine organs in insects, i.e., specialized endocrine glands; and neurosecretory cells, most of which are within the central nervous system.
- Endocrine glands are ductless glands or secretory organs of endocrine system that secrete their products, hormones, directly into circulatory system.
- Prothoracic or ecdysial glands are a pair of diffuse glands at back of head or in thorax.
- The prothoracic gland is stimulated by brain hormone to produce another hormone known as moulting hormone.
- Moulting fluid contains enzymes which digest away a portion of old cuticle and aid insect in moulting process. The cells of these glands exhibit cyclic secretory activity, reach-ing to a maximum between moults.
- The corpora allata (singular corpus allatum) are paired glandular forms, situated one on each side of oesophagus.
- The corpora allata arise from lateral ventral ectoderm in the head adjacent the root of mandibles and maxillae.
- Corpora Allata (CA) synthesize one of most essential hormones for insect development known as Juvenile Hormone (JH).
- Presence of Juvenile Hormone (JH) maintains the immature stages of insects and its absence permits development of adult through process of metamorphosis.
- The Corpora Cardiaca (CC) (singular corpus cardiacum) are a paired organ or single structure. It is placed posterior to brain and attached with aorta.
- The Corpora Cardiaca (CC) serve as main neurohemal organ in insects and secretes several types of neuropeptides or hormones. The most important neurohormones stored and secreted by corpora cardiaca is Prothoracicotropic Hormone (PTTH), earlier known as brain hormone or ecdysiotropin.
- The larvae of true flies (Cyclorrhapha: Diptera) have a small ring of tissue, held through tracheae, referred as the ring gland or Weismann's ring.

- Ring glands are formed from fusion of corpus allatum, corpus cardiacum and thoracic glands.
- Ring glands have different cells but are homologous with corpus allatum, corpus cardiacum and thoracic glands.
- Epitracheal glands are found in highly evolved insects such as butterflies, flies some beetles and bees. These glands contain 16–18 large neurosecretory cells bound to a trachea neighbouring each spiracle. The neurosecretory cells here are also called as Inka cells.
- Neurosecretory cells are present in ganglia of central nervous system. They usually look like monopolar nerve cells. They typically secrete their products into haemolymph. Somata of neurosecretory cells occur in all ganglia of central nervous system.
- Bursicon is important hormone for cuticular tanning. It is secreted from mNSC in some insects. It is principally found in abdominal ganglia and released via abdominal perivisceral organs.
- The prothoracic glands are a pair of endocrine glands located in prothorax of cockroach.
- Prothoracic gland is main source of ecdysteroids in larvae of cockroach.
- Endocrine glands of larva comprise corpora cardiaca, corpora allata and prothoracic glands.
- Corpora allata and prothoracic glands work antagonistically and are important during the process of moulting in larval stage. Prothoracic gland begins to degenerate during pre-pupal stage of development.
- The **nervous system** is a part of animal's body that coordinates its behaviour and transmits signals between different body areas
- The nervous system have two main types of specialized cells namely neurons and glial cells.
- Neurons transmit signals between cells and from one part of the body to another.
- Glial cells regulate homeostasis and provide structural and metabolic support to neurons.
- The basic component of nervous system is nerve cell also called as neuron. These are conducting cells responsible for transducing, conveying or processing nerve impulses.
- Cell body of neuron is called as soma or perikaryon or neurocyte. Cell body has nucleus, many mitochondria, Golgi complexes and Rough Endoplasmic Reticulum (RER). Cell body plays major role in protein synthesis.
- Dendrites are short, branched projections that extend from cell body.
- Dendrites receive information via several receptors situated in their membranes that bind to chemicals. These chemical messengers are known as neurotransmitters.
- Axon is a large projection that extends from cell body and functions to send information.

- Monopolar neuron are also called unipolar neurons. These have single projection from cell body. This single projection is then splits close to cell body into two trunks, one form dendrites for incoming signals and another form an axon for outgoing signals.
- Bipolar neurons have two projections that extend in opposite directions from cell body. One projection form dendrite and another become axon.
- Sensory or afferent neurons are generally bipolar but can be multipolar neurons have dendrites that are near to sense organs or receptors. They always carry information toward central nervous system.
- Motor or efferent neurons are unipolar cells that carry impulses or signals from central nervous system and stimulate responses in muscles and glands. Their cell bodies are located within a ganglion.
- Interneurons (internuncial or association) neurons transmit information from sensory to motor neurons or other interneurons.
- Local interneurons are restricted to an individual ganglion and they can be spiking or non-spiking.
- Inter-segmental interneurons convey information along nerve cord.
- Association between terminal arborisations and dendrites is called a synapse.
- Space or gap between arborisations and dendrites is called as synaptic cleft or gap.
- Pre-synaptic terminal is a specialized area that contains neurotransmitters in synaptic vesicles.
- Post-synaptic terminal is the receiving part of synapse between two neurons.
- Synaptic vesicles are small vesicles that are clustered at presynaptic terminals. They store neurotransmitters and release them by calcium-triggered exocytosis.
- Acetylcholine is known to be main prevalent excitatory transmitter in insect nervous system. This is chief transmitter of olfactory and mechanosensory neurons and of numerous interneurons.
- Glial cells are non-conducting supporting cells which enclose neurons and support to protect neurons and maintain stable ionic environment.
- The perineurium and neural lamella are collectively known as the nerve sheath.
- Neuropile is a central region consisting of intermingling, synapsing axons encapsulated by processes of glial cells, called as neuropile.
- Nerve cells are found grouped in bundles. Axons are primary transmission lines of nervous system and as bundles they form nerves. Thus, a nerve is a bundle of dendrites or axons that serve same part of body.
- The cell bodies of interneurons and motor neurons are grouped, with fibres (axons and dendrites) interconnecting all types of nerve cells to form nerve centers are known as ganglia.
- The Central Nervous System (CNS) is main part of nervous system. It

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consists of a series of ganglia which are joined together by longitudinal (connectives) and transverse (commissure) cords of nerve fibres.

- The protocerebrum is largest and complex part of brain and bi-lobed in appearance. It contains both neural and endocrine (neurosecretory) elements.
- The optic lobes are lateral extensions of protocerebrum to compound eyes. Each contains three successive neuropiles called as lamina, medulla and lobula complex.
- Deutocerebrum is fused ganglia of antennary segment. Deutocerebrum consists of antennal (with olfactory function) lobes and antennal mechanosensory and motor center.
- Thoracic ganglia control the organs of locomotion. Each of thoracic ganglia has two pairs of principal nerves, one pair of which provides the common musculature of its segment and the other pair innervates the muscles of the legs.
- Each abdominal ganglion has a pair of principal nerves that supply to the muscles of its segment. The abdominal ganglia are variable in number.
- Ventral sympathetic system consists of a pair of transverse nerves involved with each ganglion of ventral nerve cord, and each pair is connected with ganglion preceding it by a median longitudinal nerve.
- Peripheral Nervous System (PNS) includes an extremely delicate network of nerve fibres and multipolar nerve cells located in integument. The peripheral nervous system consists of all of the motor neuron axons that radiate to the muscles from the ganglia of the CNS and stomodeal nervous system.
- Neurotransmitters are the chemical involved in impulse conduction through synaptic gap.
- Eye is visual organ or photoreceptor and capable of recording form, colour differences or movements in external objects. Insect eyes are always located on the head and the optic centers lie in protocerebral parts of brain.
- In exopterygote insects, young resemble adults but have externally developing wings. They undergo modest change between immature and adult, without going through pupal stage. This is called hemimetabolism or incomplete metamorphism.
- Endopterygote insects, also known as Holometabola, develop wings inside body and undergo an elaborate metamorphosis involving a pupal stage. This is called as holometabolism or complete metamorphism.
- Dioptric apparatus transmits and condenses impinging light rays upon receptive surface. It always includes cuticle in the form of lens, largely formed by specialized cells of optic epidermis.
- Receptive apparatus consists of sensory cells forming retina, which present specialized receptive surfaces at points where light rays are focused and are continued directly into optic nerve.
- The dorsal ocelli (singular ocellus) are simple eyes of adult insects in addition to compound eyes and of exopterygote larvae and nymphs.

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- In eucone eyes each ommatidium contains a true crystalline cone, which is a hard refractive body formed as an intracellular product of cone cells.
- In pseudocone eyes type of eye, there is no true crystalline cone and the four cone cells are filled with a transparent, semiliquid material.
- In acone eyes, there is a group of elongate, transparent cone cells but the latter do not secrete any kind of cone whether crystalline or liquid.
- In exocone eyes, crystalline cone is replaced by a cone of extracellular, cuticular material which appears as a deep ingrowth from inner of corneal facet.
- The eye's ability to detect form of an object depends on its resolving power.
- Visual tracking refers to an animal's ability to keep a moving target within a specific area of retina, and also when animal itself is moving.
- When a ray of light comes back into the same medium after striking the surface of another medium then the phenomenon is called reflection of light.
- The change of direction and speed of light as it enters from one medium to another is termed as refraction of light.
- A *mosaic* is a combination or merge of two or more *images*.
- Inverted image means the image is upside down compared to the object.
- An erect image appears right-side up. The word erect means upright or straight.
- Dorsal ocelli are built upon a plan just similar to that of the human eye than insect compound eye.
- Transformation of light to electrical energy involves visual pigment rhodopsin. Phototransduction cascade leads to transformation of rhodopsin to active metarhodopsin.
- Compound eyes are a pair of large, sessile, compound eyes in the form of black, kidney-shaped organs on lateral sides of head. Each consists of about 2,000 visual elements or units, called ommatidia.
- Insects produce special sounds, receive these sounds through sense-organs and react to them with appropriate behaviour patterns.
- Sound is produced either by rubbing one part of body to another part or one part by other external object.
- A single insect species can make several sounds, each with its own function.
- Sounds and songs of different kinds and intensities are produced by a number of species in insects.
- Sound is produced when an object's vibrations move through a surrounding medium, i.e., air, water, or solid.
- Sound travels in waves and are composed of compression and rarefaction patterns.
- Compression happens when molecules are densely packed together.
- Frequency is number of sound waves produced each second.
- Amplitude of a sound wave determines its relative loudness.

- Pitch refers to the quality that enables us to judge sounds as being higher and lower. A high-pitched sound causes molecules to rapidly oscillate, while a low-pitched sound causes slower oscillation.
- Oscillation is the movement back and forth in a regular rhythm.
- Wavelength is distance that wave travels before it repeats itself. Wavelength itself is a longitudinal wave that shows compressions and rarefactions of sound wave.
- Stridulation refers to production of vibrations by moving a cuticular ridge on one body part over a toothed ridge on another. Cuticular ridge is called as scraper or plectrum and a toothed ridge is known as file or strigil.
- A trill is defined as a continuous train of notes or pulses given too fast to count and usually lasting several seconds or more. Pulses slow enough to be discerned, for example jumping bush cricket.
- A chirp is a very short bundle of rapid and irregular notes (a very short trill lasting a fraction of a second).
- Courtship singing enables insects to accomplish mating and thereby spermatophore is transferred to female.
- Sensillum plural sensilla is an insect sensory organ protruding from cuticle of exoskeleton, or lying within or below it.
- Sensilla occur as small hairs or pegs over an individual's body. Inside each sensillum there are two to three sensory neurons. These neurons, or receptors, gather information about environment.
- Sensilla are divided into two broad categories namely hair-like structures or hair sensilla and campaniform sensilla.
- In aporous sensilla there are no pores except molting pore, in the cuticle of hairs and perform specially as mechanoreceptors and thus these hairs are called as aporous sensilla.
- When the hairs taper from base to tip, they are referred as trichoid sensilla. Several of these sensilla are sensitive to touch through deflection.
- Stretch receptors attach to connective tissue and other end connected with body wall/ intersegmental membrane/ muscle and associated with multipolar neurons.
- Coupling is the deformation of sensory neuron's dendritic membrane caused by movement of hair in its socket, the inward movement of the cuticular dome in campaniform sensilla, or the stretching of the chordotonal sensillum.
- Transduction is the generation, followed by its flow through the dendritic membrane, of the receptor (generator) current. It results from the stretching of the membrane and the opening of transduction (stretch-activated) channels contained therein.
- Muscle is excitable and contractile tissue of animals which is responsible for body movement.
- Each muscle is made up of varied number of fibers. They are long and multinucleate cells running entire length of muscle.

2.10 KEY TERMS

NOTES

- **Neuron:** The basic component of nervous system is nerve cell also called as neuron.
- **Dendrites:** Dendrites are short, branched projections that extend from cell body.
- **Axon:** Axon is a large projection that extends from cell body and functions to send information.
- **Synapse:** Association between terminal arborisations and dendrites is called a synapse.
- **Synaptic cleft:** Space or gap between arborisations and dendrites is called as synaptic cleft or gap.
- **Pre-synaptic terminal:** Pre-synaptic terminal is a specialized area that contains neurotransmitters in synaptic vesicles.
- **Post-synaptic terminal:** Post-synaptic terminal is the receiving part of synapse between two neurons.
- **Synaptic vesicles**: Synaptic vesicles are small vesicles that are clustered at presynaptic terminals.
- **Neuropile:** Neuropile is a central region consisting of intermingling, synapsing axons encapsulated by processes of glial cells, called as neuropile.
- **Neuromuscular junction**: A fluid-filled space between tip of motor axon and muscle cell membrane called a neuromuscular junction.
- **Reflection:** When a ray of light comes back into the same medium after striking the surface of another medium then the phenomenon is called reflection of light.
- **Refraction:** The change of direction and speed of light as it enters from one medium to another is termed as refraction of light.
- **Single mosaic image:** A *mosaic* is a combination or merge of two or more *images*.
- **Inverted image**: Inverted image means the image is upside down compared to the object.
- **Upright image:** An erect image appears right-side up. The word erect means upright or straight.
- **Frequency:** Frequency is number of sound waves produced each second.
- **Amplitude:** Amplitude of a sound wave determines its relative loudness.
- **Pitch:** Pitch refers to the quality that enables us to judge sounds as being higher and lower.
- **Oscillation:** Oscillation is the movement back and forth in a regular rhythm.
- **Wavelength:** Wavelength is distance that wave travels before it repeats itself.
- **Intensity:** Intensity is power per unit area carried by a sound wave.

2.11 SELF-ASSESSMENT QUESTIONS AND EXERCISES

NOTES

Short-Answer Question

1. What is ecdysial gland?
2. What are neurosecretory cells?
3. How is secretion in corpora allata conducted?
4. Write about secretion and function of Corpora cardiaca.
5. Define the following terms:
   i. Neurohemal organs
   ii. Axon
   iii. Dendrites
   iv. Glial cells
   v. Dorsal ocelli
   vi. Chordotonal organs.
6 Give structural classification of neuron.
7 Write short note on mushroom bodies.
8 Name different visual organs in insects.
9 Explain briefly about the sensory receptor in ommatidium.
10 What are sound producing organs in insect?
11 Name various mechanisms of sound production in insects.
12 Write in brief about ring glands.
13 What do you understand by percussion?
14 List the various types of mechanoreceptors in insects.
15 What is mechanical stimuli?
16 What are perireceptor events for olfactory sensillum?
17 Brief a note on olfactory receptors.
18 What are gustatory receptors?
19 Give a brief note on T-system.
20 What is muscle insertion and how is it conducted?
21 Discuss the categories of muscles in insects.

Long-Answer Question

1. Discuss about neuroendocrine secretion in insects and its function in detail.
2. Elaborate a note on Endocrine Glands.
3. What are neurosecretory cells? Explain different types of variations in neurosecretory cells.
4. Explain the secretions and functions of neurosecretory cells.

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5. Illustrate with the help of well labelled diagram the role of neuroendocrine secretions in moulting and metamorphosis in butterfly.
6. Explain with the help of table various types of hormones, their source, target and functions in insects.
7. Discuss about the general plan of nervous system in insects.
8. Explain the basic components of nervous system.
9. Elaborate a note on division and physiology of nervous system.
10. Draw a well labelled diagram to show different types of neurons based on number of projections.
11. Discuss about the different types of visual organs in insects.
12. Elaborate a note on structure of various visual organs.
13. Analyse the physiology of vision.
14. Discuss about sound production in insects.
15. Elaborate a note on mechanism of sound production.
16. What are different types of songs that insects produce? Explain their significance.
17. Elaborate a note on mechanoreceptors and chemoreceptors.
18. Discuss about the basic structures of sensilla.
19. Explain the physiology of various types of mechanoreceptors and chemoreceptors.
20. Discuss about the muscles in insect.
21. Elaborate a note on structure of various types of muscles.
22. Write a descriptive note on physiology of muscles.

2.12 FURTHER READINGS

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UNIT 3 BIOLUMINESCENCE, PHEROMONES, NERVOUS INTEGRATION, DIAPAUSE, MIMICRY AND INSECT BEHAVIOUR

Structure

3.0 INTRODUCTION

Bioluminescence is defined as the emission of light from a living organism that performs some biological function. Bioluminescence is one of the oldest fields of scientific study almost dating from the first written records of the ancient Greeks. When a living organism produces and emits light as a result of a chemical reaction, the process is known as bioluminescence - bio means 'living' in Greek while lumen means 'light' in Latin. During the process, chemical energy is converted into light energy. The process is caused by an enzyme-catalyzed chemoluminescence reaction. Bio luminescence is a product of a chemical reaction in an organism. It involves a class of chemicals called luciferins (light bringers). The luciferin oxidizes in the presence of a catalytic enzyme (luciferase) to create light and an ineffective compound. Bioluminescence serves various purposes, including sexual attraction and courtship, predation and defense.

A pheromone is a secreted or excreted chemical factor that triggers a social response in members of the same species. Pheromones are chemicals capable of acting like hormones outside the body of the secreting individual, to impact the behaviour of the receiving individuals. There are alarm pheromones, food trail pheromones, sex pheromones, and many others that affect behaviour or physiology. Pheromones are used by many organisms, from basic unicellular prokaryotes to complex multicellular eukaryotes. Their use among insects has been particularly well documented. In addition, some vertebrates, plants and ciliates communicate by using pheromones. The ecological functions and evolution of pheromones are a major topic of research in the field of chemical ecology. The word pheromone was coined by Peter Karlson and Martin Lüscher in 1959. Pheromones are also sometimes classified as ectohormones. They were researched earlier by various scientists, including Jean-Henri Fabre, Joseph A. Lintner, Adolf Butenandt, and ethologist Karl von Frisch who called them various names, like for instance 'alarm substances'. 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 signalling, immune system changes and/or behavioural change in the recipient. They proposed the term to describe chemical signals from conspecifics that elicit innate behaviour soon after the German biochemist.

In biology, the classical doctrine of the nervous system determines that it is highly complex part of an animal that coordinates its actions and sensory information by transmitting signals to and from different parts of its body. The nervous system detects environmental changes that impact the body, then works in tandem with the endocrine system to respond to such events. Nervous tissue first arose in wormlike organisms about 550 to 600 million years ago. However, this classical doctrine has been challenged in recent decades by discoveries about the existence and use of electrical signals in plants. On the basis of these findings, some scientists have proposed that a plant nervous system exists and that a scientific field called plant neurobiology should be created. This proposal has led to a dispute in the scientific community between those who think we should talk about the nervous system of plants and those who are against it. The inflexibility of the positions in the scientific debate on both sides has led to proposing a solution to the debate, consisting of redefining the concept of the nervous system by using only physiological criteria and avoiding phylogenetic criteria. The nervous system consists of the brain, spinal cord, sensory organs, and all of the nerves that connect these organs with the rest of the body. Together, these organs are responsible for the control of the body and communication among its parts. The brain and spinal cord form the control center known as the Central Nervous System (CNS), where information is evaluated and decisions made. The sensory nerves and sense organs of the Peripheral Nervous System (PNS) monitor conditions inside and outside of the body and send this information to the Central Nervous System (CNS).

Diapause is a period of suspended or arrested development during an insect's life cycle. Insect diapause is usually triggered by environmental cues, like changes in daylight, temperature, or food availability. Diapause may occur in any life cycle stage—embryonic, larval, pupal, or adult—depending on the insect species. Insects inhabit every continent on Earth, from the frozen Antarctic to the balmy tropics. They live on mountaintops, in deserts, and even in the oceans. They survive frigid winters and summer droughts. Many insects survive such extreme environmental conditions through diapause. When things get tough, they take a break. Diapause is a predetermined period of dormancy, meaning it is genetically programmed and involves adaptive physiological changes. Environmental cues are not the cause of diapause, but they may control when diapause begins and ends. Quiescence, in contrast, is a period of slowed development that is triggered directly by environmental conditions, and that ends when favourable conditions return.

In nature, some animals have evolved really clever tactics to avoid becoming something else's snack. These adaptations can include behavioural traits to scare away predators or anatomical adaptations to give these animals an advantage in evading their pursuers. Adaptations in coloration and body shape to either stand out or blend in help organisms survive the perils of life in the wild. Some animals present bright colours to warn predators that trying to pursue them might not be such a good idea, while others have perfected the art of not being seen or fooling others into thinking they are something else. While these traits and tactics are found throughout the animal kingdom, invertebrates showcase these adaptations in some truly amazing ways. Their deception schemes take on many forms that confuse potential predators and make casual observers and even well-trained eyes take a second look. Some animals mimic others as a way to protect themselves from predators. There are many forms of mimicry. Animals that are mimics develop traits to either look, sound, smell or behave like something else. Some mimics (insects in particular) have evolved to look like other predators, and others have evolved bodies that resemble completely different organisms and objects. One example of mimicry in insects is the monarch and viceroy. Monarchs feed entirely on milkweed that makes them toxic to predators. Viceroys are also unpalatable since they sequester salicylic acid from the foods eaten by caterpillars that include plants of the willow family. In this case, their similarly the evolved bright orange and black coloration makes them quite visible and their shared predators know to avoid them in benefiting both species.

Social insects, such as termites, ants and many bees and wasps, are the most familiar species of eusocial animals. They live together in large well-organized colonies that may be so tightly integrated and genetically similar that the colonies of some species are sometimes considered superorganisms. It is sometimes argued that the various species of honey bee are the only invertebrates to have evolved a system of abstract symbolic communication where a behaviour is used to represent and convey specific information about something in the environment. In this communication system, called dance language, the angle at which a bee dances represents a direction relative to the sun, and the length of the dance represents the distance to be flown. Though perhaps not as advanced as honey bees, bumblebees also potentially have some social communication behaviours. Only insects that live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to several kilometers distance. In a phenomenon known as philopatry, insects that hibernate have shown the ability to recall a specific location up to a year after last viewing the area of interest. A few insects seasonally migrate large distances between different geographic regions.

In this unit, you will study about bioluminescence, light producing organs, mechanisms and its significance, pheromones types, chemical nature and function, nervous integration, learning and memory, diapause in insects, mimicry in insects and their behaviour social life, symbiosis and adaptations.

3.1 OBJECTIVES

After going through this unit, you will be able:

- Understand about bioluminescence, its mechanisms and significance
- Analyse about light producing organs
- Discuss about pheromones types, its chemical nature and function
- Explain the nervous integration in insects
- Describe learning and memory in insects
- Discuss about diapause in insects
- Understand about mimicry in insects
- Elaborate on insect behaviour, their social life, symbiosis and adaptations

3.2 BIOLUMINESCENCE: LIGHT PRODUCING ORGANS, MECHANISMS AND ITS SIGNIFICANCE

Bioluminescence is an amazing natural phenomenon in which an organism produces and emits light due to a chemical reaction where the chemical energy is converted into light energy.

Origin of Bioluminescence

The Greeks and Romans were the first to report the characteristics of luminous organisms. Aristotle (384-322 BC) described 180 marine species and was the first to recognize 'cold light'. The Greeks also made reference to sea phosphorescence (about 500 BC). Later in 19th century Raphael Dubois performed a significant experiment where he extracted the two key components of a bioluminescent reaction and was able to generate light. He coined the terms 'luciferine' and the heat labile luciferase. The first luciferin was isolated in 1956.

Definition

Bioluminescence can be defined as the emission of light by a living creature for the purpose of survival or reproduction. It is a cool light produced by a biological mechanism involving chemical activities that are often unique to that organism. Bioluminescence is one of the principal communication systems in deep sea, and it occurs mostly in the marine environment. Bioluminescence is caused by a chemoluminescence reaction in which the pigment luciferin is catalysed by the enzyme luciferase. The majority of reactions make use of energy. The reaction can occurs inside or outside the cell. Many species produce luciferase, which helps in the speeding up of reactions. Some organisms bind oxygen with luciferin in a photoprotein. It lights up the moment some ion is present.

Structure of Luciferin

Luciferins are a class of light-emitting heterocyclic compounds named after the Latin word lucifer, which means 'light bringer'. Luciferins are a type of small molecule substrate that are oxidised by the enzyme luciferase to produce oxyluciferin and light energy (Refer Figure 3.1). Although the number of different forms of luciferins is unknown.

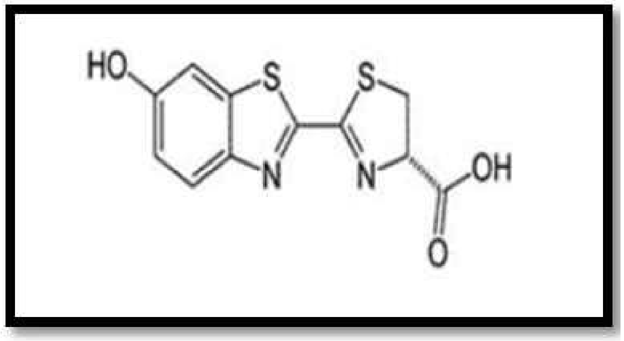


Fig. 3.1 *Structure of Luciferin*

Bioluminescence in Insects

Some terrestrial arthropod groups display true or self-luminescence. The order Coleoptera is the largest bioluminescent group, with several species that are known to have highly developed photogenic organs, including the Firefly (*Lampyridae*), Click beetle (*Elateridae*), Railroad worm (*Phengodidae*), Rove beetle (*Staphylinidae*), and other related families, which are primarily used for mating and defense. The light emission is also best known in Dipteran (Fungus gnat), Hemiptera (Spotted lanternfly) and Collembola (Springtails). To find partners, fungus gnat males orient towards adult female and pupal lights, while the maggot produces light to brighten their environment and attract possible meals. The pigment firefly luciferin, which is found in many Lampyridae species and is responsible for fireflies unique yellow light emission, is found in many Lampyridae species. Because the females of some Lampyridae species are wingless and sedentary, light generation is critical for attracting the winged male.

Some Important Insect Orders Depicting Bioluminescence

Some insects that have bioluminescence are as follows:

Coleoptera (Beetles)

The beetles have the largest number and variety of luminescent species. They are found mainly in the superfamily Elateroidea, which includes Fireflies (*Lampyridae*), Railroad worms (*Phengodidae*), Click beetles (*Elateridae*), and related families. Luminescence is also found in a luminescent larva of *Xantholinusin*. Fireflies emit green-yellow flashes characterized by duration, interval, and frequency from ventral lanterns for sexual attraction purposes. Click beetles have two dorsal prothoracic lanterns, which usually emit continuous green light, and a ventral abdominal light organ that emits continuous green-orange light when the insect is flying. Railroad worms emit the widest range of colors among luminescent beetles, including some of the most spectacular examples with larvae and females having rows of lateral lanterns along the body emitting green-orange light and, in addition South-American species with cephalic lanterns emitting from yellow-green to red light depending on the species. In the larval stage, bioluminescence assumes mainly defensive functions but attraction of prey is also seen in the larvae of the Brazilian *Pyrearinuster mitilluminans* Click beetle, which display the phenomenon of luminous termite mounds.

Glowworm

As per the name, glow worms are not worms inherently, instead they are larvae of different groups of adult females or insects that have a resemblance to the larvae. The adult versions of these glowworms do not possess wings, instead they exhibit structures on their abdominal and thoracic areas, wherein these organs emit light. They use the process of bioluminescence to lure their mates and attract their prey, such as bugs. They hang suspended to the sticky long fibres they produce wherein the prey are entrapped. In order to warn predators, glow worms emit light that is toxic enough.

Fireflies

Fireflies have light-generating structures located in their abdomens wherein light is generated when the chemical luciferin reacts with calcium, oxygen, ATP and the enzyme responsible for the bioluminescence, luciferase, inside the organ. It serves quite a few purposes, such as in adult fire-flies, bioluminescence is used to lure mates and attract prey. The light pattern that flashes is helpful in identifying different members belonging to the same species, also to discriminate between female and male fireflies. In the larvae version of the firefly, it is used as a warning to the predators so as to not consume them as they possess toxic elements. Some other fireflies have the ability to sync their light emission to a process referred to as simultaneous bioluminescence.

In Table 3.1 bioluminescent colour variation in insect is shown.

Table 3.1 *Bioluminescent Color Variation in Insect*

Insect Groups	Color Variations
Phengodids Glow-worms (*Phengodidae*)	Paired green lights on each segment and red lights at the end.
Mycetophilidae (*Arachno campa*)	Blue green light.
Fulgoridae (Lantern fly)	White light.
Lampyridae (Photinusand Lampyris)	Yellow-green in color (520-650 nm).
Phengodidae, Railroad worm (*Phrixothrix*)	Larval and adult female, thorax and abdomen produce green to orange light (530-590 nm), on head produces red light (580 nm to over 700 nm).

3.2.1 Mechanisms of Bioluminescence

A French physiologist, demonstrated that three substances are involved in bioluminescence: **luciferin**, **luciferase** and **molecular oxygen**. Luciferin, which is secreted by photocytes, is a low molecular weight compound that may be an aldehyde, a polypeptide complex or a protein. Light is produced by the oxidation of Lucifer in the presence of the enzyme luciferase. Bioluminescence is due to the substrate enzyme complex of luciferin-luciferase within the cellular cytoplasm. These luciferin-luciferase complexes differ in structure among species. ATP first activates luciferin in the presence of magnesium (Mg^{2+}) and luciferase to produce adenylluciferin, which is then oxidized to form excited oxyluciferin. During the enzymatic oxidation of luciferin large amounts of energy become available in a single step, so that the product of the reaction is left in a highly excited state. This product emits light when the excited state returns to the ground state (Refer Figure 3.2).

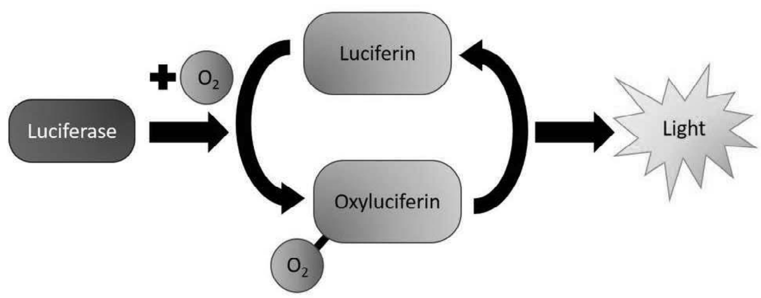


Fig. 3.2 *Bioluminescence Mechanism*

The reaction is very efficient, some 98% of the energy involved being released as light without production of heat. Instead of a luciferase, the jellyfish Aequorea victoria makes use of another type of protein called a photoprotein, in this case specifically aequorin. When calcium ions are added, rapid catalysis creates a brief flash quite unlike the prolonged glow produced by luciferase. In a second, much slower step, luciferin is regenerated from the oxidized (oxyluciferin) form, allowing it to recombine with aequorin, in preparation for a subsequent flash. Photoproteins are thus enzymes, but with unusual reaction kinetics. Furthermore, some of the blue light released by aequorin in contact with calcium ions is absorbed by a green fluorescent protein, which in turn releases green light in a process called resonant energy transfer.

3.2.2 Significance of Bioluminescence in Insects

Bioluminescence is assumed to have functional relevance in primitive forms of life. For example, in many arthropods, the light from bioluminescence is used to attract the opposite sex for mating, to attract prey, or it may be used for defense.

Mating Signal

In firefly, light is used as a mating signal. In some species, bioluminescence induces members of the same species to congregate, enhancing mating chances indirectly. Because the females of some Lampyridae species are wingless and sedentary, light production is critical for them to attract winged males. Bioluminescent insect flash patterns differ between species and sexes. Some species wait 5.5 seconds before emitting a single brief flash on a reasonably chilly night. Other animals may hold the flash for a full second after waiting one second. A significant number of tropical species converge and flash in unison. Male and female fireflies of *Photinus pyralis* commonly known as common eastern fly emerge at dusk emitting a single short flash at regular intervals. The flashes are usually from male fireflies seeking mates. Males outnumber the females fifty to one. Females climb a blade of grass, flashing when males flash within 10-12 feet of the females. Exchange of signals is repeated 5 to 10 times until they start mating.

Predation

The most unique example of light acting as a lure for prey is found in the New Zealand glowworm fly, known as *Arachnocampa luminosa*. The female fly deposits eggs on the ceiling of dark caves. Upon hatching, the larvae hang down by a sticky thread and produce light. During night, the entire cave may glow with this light, attracting other insect species. These attracted insects get entangled in the sticky threads and are preyed upon by the larvae. The caves inhabited by flies are popularly known as luminous caves and are tourist attraction spots in New Zealand.

Defense

The constant glow of the head area in Railroad worm larvae while walking supports an illumination role, but the circumstances in which the lateral light organs are turned on suggest a defense function. Potential predators are deterred by sudden flashes. The railroad worm larvae live in great densities and are confined to small areas. They may employ simultaneous emission to terrify possible adversaries or to warn mated females about to lay eggs about congestion and competition for food supplies.

Bioluminescence in Pest Management

Bioluminescence is used to map the distribution patterns of organisms. In 2001, scientists in the United States injected Green Fluorescent Protein (GFP) obtained from the jelly fish *Aequorea victoria* (also called as crystal jelly) into the genetic material of the pink bollworm, a cotton pest. When observed at its larval stage, the GFP transgenic pink bollworm strain fluoresces brightly green. This study has two goals: the first is to create a GFP-tagged pink bollworm strain for field experiments and the second is to map the pest's range. It could also be used as a supplement by field managers. Their future objective is to eventually add a temperature-sensitive lethal gene along with the GFP gene into the pink bollworm that could be used for its management.

Check Your Progress

1. Define the term bioluminescence.
2. What are luciferins?
3. Name some insect that have bioluminescence.
4. Give the significance of bioluminescence.

3.3 PHEROMONES: TYPES, CHEMICAL NATURE AND FUNCTION

Communication among animals is essential for their well-being. Almost all animals communicate through chemicals produced by glands within the body. Pheromone is a chemical that is produced and released into the environment by an animal which affects the behaviour of another animal of the same species.

Karlson and Luscher (1959) coined the term pheromone, which is derived from two Greek words: pherein, to carry and harman, to excite. The term was originally assigned to insect sex attractants, but it was later broadened to include a variety of chemicals released into the environment that have varied functions in practically all animals.

Pheromones are substances that are created as messengers and influence the behaviour of other insects or animals. They are primarily carried by the wind, although they can also be deposited in soil, vegetation or other objects. When pheromones are delivered in different combinations or concentrations, they can send out diverse signals. Pheromones differ from visual or auditory cues in several ways. They travel slowly, do not dissipate rapidly, and have a vast range of effectiveness. Pheromone detection does not require sound or vision receptors, and pheromone direction is not confined to straight lines.

Pheromones are unique to each species. Hormones released by exocrine glands are the most common type. Pheromones (also known as ectohormones) are chemical messengers that are employed as chemo-signals in intra-specific communication. They are released in small amounts but have a big impact.

Discovery of Pheromones

Pheromones were discovered by accident in the 18th century. Bonnet, a French biologist, discovered the ant trail. Bonnet set up an ant colony on one end of a table and a small pile of sugar on the other.

He noticed that ants coming out of the colony moved across the table to the pile, picking up sugar and moving back to the colony with it. The ants moved to and fro along a definite track, with none diverting from it.

Bonnet was curious as to why the ants followed such a distinct path, so he broke the continuity of this path by rubbing his finger across the line of the ants. The ants stopped and searched the rubbed area. They tapped their antennae on the ground while waving them in the air.

Subsequently, a few adventurous ants ran across the rubbed area. After that, the ants from both sides met, recognised each other and resumed their trek. As a result, Bonnet deduced that the ant's journey was actually a trail of chemicals that the ants could detect and follow (Refer Figure 3.3).

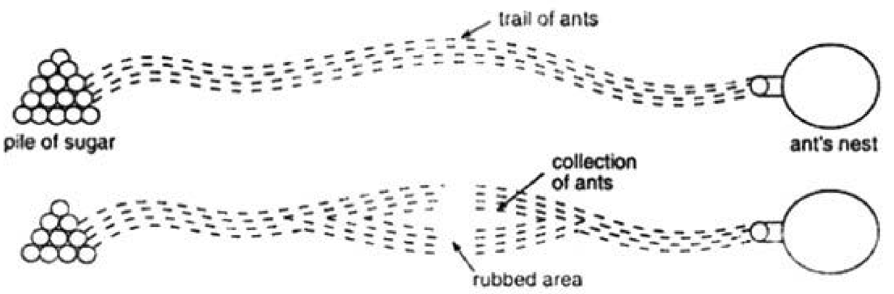


Fig. 3.3 *Bonnet Experiment with Ants*

In 1953, the first pheromone was discovered, i.e., Bombykol. Bombykol is a pheromone released by the female silkworm moth to attract mates. This signal is effective at low concentrations and can travel long distances.

3.3.1 Chemical Nature of Pheromones

Pheromones are chemical in nature. Chemical signals are particularly well-developed in insects and mammals. These chemical signals may be either volatile or non-volatile. Some chemical signals are designed to last only for a short time and hence, are volatile. They tend to have low molecular weights. Example of such volatile chemical signals are the chemicals used by ants to signal alarm which fades within a minute or even less.

Other type of chemical signals are designed to last for a longer time which allows a message to persist even in the absence of the signaller. Such chemical signals are said to be non-volatile. Examples of such nonvolatile chemical signals are the territory marker pheromones of spotted hyaena which is secreted by sub-caudal scent glands.

Pheromones isolation and extraction is a laborious work. The sex attractant of Cockroaches (*Periplaneta americana*) was identified by Robert T. Yamomoto. He isolated it from a vapour emitted by female cockroaches, by running a stream of air through large cans containing thousands of females, for a period of eight months. The vapour was trapped by freezing it with dry ice.

From such laborious work Yamomoto was able to extract only 12-2 mg of pure sex attractants. This pheromone was identified as 2, 2-dimethyl 3-iso-propylidene cyclopropyl propionate, which is a volatile yellow coloured substance having a strong floral odour. Male cockroaches are attracted by this odour and respond by rais-ing their wings and making mating attempts.

Similar type of work was also done on female Silk moth (*Bombyx mori*), where from the abdomens of five million females only 12 mg of the pure pheromone, termed as bombykol, was obtained. Other attractants which has been extracted are gyplure (gypsy moth), queen substance (honey bee), civetone (civet), muscone (musk deer). The chemical composition of various pheromones extracted from different animals are listed in Table 3.2.

Table 3.2 *Sources and Chemical Composition of Pheromones Extracted From Various Animals*

Sr. No	Animal Types	Source	Chemical Composition
1.	Tropical bug	Special duct in male	2-hexenol acetate
2.	Ant	Abdominal gland	Formic acid
3.	Honey bee	Mandibular glands of queen	$C_{10}H_{10}O_3$(9-Keto-2-decenoic acid)
4.	Silk moth	Lateral glands in female abdomen	$C_{10}H_{30}$0-Trans-1-Cis-12-hexadecadienol (Bombykol)
5.	Gipsy moth	Do	$C_{18}H_{34}O_3$(10-acetoxy-1-hydroxycis-7-hexadecane)
6.	Cockroach	Corpora allata of female	2,2-dimethyl 3-isopropylidene cyclopropyl propionate

3.3.2 Types of Pheromones

Following are the types of pheromones:

- Aggregation Pheromones
- Alarm Pheromones
- Epideictic Pheromones
- Releaser Pheromones
- Primer Pheromones
- Signal Pheromones
- Territorial Pheromones
- Trail Pheromones
- Information Pheromones

i. Aggregation Pheromones

Aggregation pheromones are produced by one or the other sex, these pheromones attract individuals of both sexes. Its roles include predator defense, partner selection and mass attack to overcome host resistance. Aggregation refers to a collection of people gathered in one place, whether they are of one gender or both. Because they frequently result in the attendance of both sexes at a calling location and an increase in density of conspecifics surrounding the pheromone source, male-produced sex attractants have been dubbed aggregation pheromones. Females create the majority of sex pheromones, while males produce only a small percentage of sex attractants.

ii. Alarm Pheromones

Some species release a volatile substance when attacked by a predator that can trigger flight (in aphids) or aggression (in bees) in members of the same species.

Insects are members of the same species. When an ant detects the alarm pheromone, it can either flee or freeze and act dead, or it can race towards the source of the fragrance and attack any surrounding opponents. Different alarm pheromones in ants are likely to cause such a wide range of responses. The diversity of signals in the alarm pheromones of the weaver ant, *Oceophylla longinoda*, is attributed to over 30 distinct compounds. The alarm pheromones of the weaver ant cause a cascade of responses in its nestmates.

Unless additional amounts of the alarm pheromone are released, it soon dissipates. This ensures that once the emergency is over, the ants return quietly to their former occupations.

Honeybees also have an alarm pheromone (which is a good thing not to elicit around a colony of 'Africanized' bees).

iii. Epideictic Pheromones

Epideictic pheromones are different from territory pheromones, when it comes to insects. Fabre observed and noted how females who lay their eggs in fruits deposit these mysterious substances in the vicinity of their clutch to signal to other females of the same species they should clutch elsewhere.

Sex Attractants: Hundreds of pheromones are known with which one sex (usually the female) of an insect species attracts its mates. Many of these sex attractants, or their close chemical relatives are available commercially.

They have proved useful weapons against insect pests in two ways:

- **Male Confusion:** Distributing a sex attractant throughout an area masks the insect's own attractant and thus may prevent the sexes getting together. This communication disruption has been used successfully against a wide variety of important pests. For example, the sex attractant of the cotton boll weevil has reduced the need for conventional chemical insecticides by more than half in some cotton- growing areas.
- **Insect Monitoring:** Insect sex attractants are also valuable in monitoring pest populations. By baiting traps with the appropriate pheromone, a build-up of the pest population can be spotted early.

iv. Signal Pheromones

Signal pheromones that can cause short term changes, such as the neurotransmitter release which activates a response. For instance, GnRH molecule functions as a neurotransmitter in rats to elicit lordosis behaviour.

v. Primer Pheromones

Primer pheromones trigger a change of developmental events.

vi. Trail Pheromones

Trail pheromones are common in social insects. For example, ants mark their paths with these pheromones, which are 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, the pheromone trail will be continually renewed. The pheromone must be continually renewed because it evaporates quickly. When the supply begins to dwindle, the trail making ceases. In at least one species of ant, trails that no longer lead to food are also marked with a repellent pheromone.

vi. Territorial Pheromones

Territorial pheromones are laid down in the environment and mark the boundaries of an organism's territory. In cats and dogs, these hormones are present in the urine, which they deposit on landmarks serving to mark the perimeter of the claimed territory.

viii. Information Pheromones

Information pheromones are indicative of an animal's identity or territory. For example, dogs and cats deposit chemicals in and around their territory, which then serve as an indicator for other members of the species about the presence of the occupant in that territory.

ix. Sex Pheromones

In animals, sex pheromones indicate the availability of the female for breeding. Male animals may also emit pheromones that convey information about their species and genotype. Many insect species release sex pheromones to attract a mate and many lepidopterans can detect a potential mate from as far away as 10 km (6.2 miles).

Pheromones can be used in gametes to trail the opposite sex's gametes for fertilization. Pheromones are also used in the detection of oestrus in sows. Boar pheromones are sprayed into the sty, and those sows which exhibit sexual arousal are known to be currently available for breeding.

Glands Producing Pheromones

Pheromones are produced by defi-nite glands. These glands vary in their structure and location on the body of animals.

Such glands pro-ducing pheromones are extensively studied in case of insects:

i. **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.

ii. **In Lepidoptera:** The males of Lepidopteras (butterflies and moths) produce scent from glands known as androconia which are located in wings asso-ciated with scales. Androconia have a somewhat elongated structure and terminates in a row of fine processes called fimbriae (Refer Figure 3.4). Pheromones produced by these glands evaporate through these fimbriae.

In Figure 3.4 pheromones producing glands in insects in shown, in which A. shows *Androconia* of butterflies and moths, B. shows scent cups of *Amauris* male, C. shows invaginated scent glands in *Plaodia,* D. shows mandibular gland of honey bee, E. shows Nassanoff's gland of honey bee, F. Sacculi lateralis of silk moth; and G shows (a) and (b) top and side view of scent producing glands in ants.

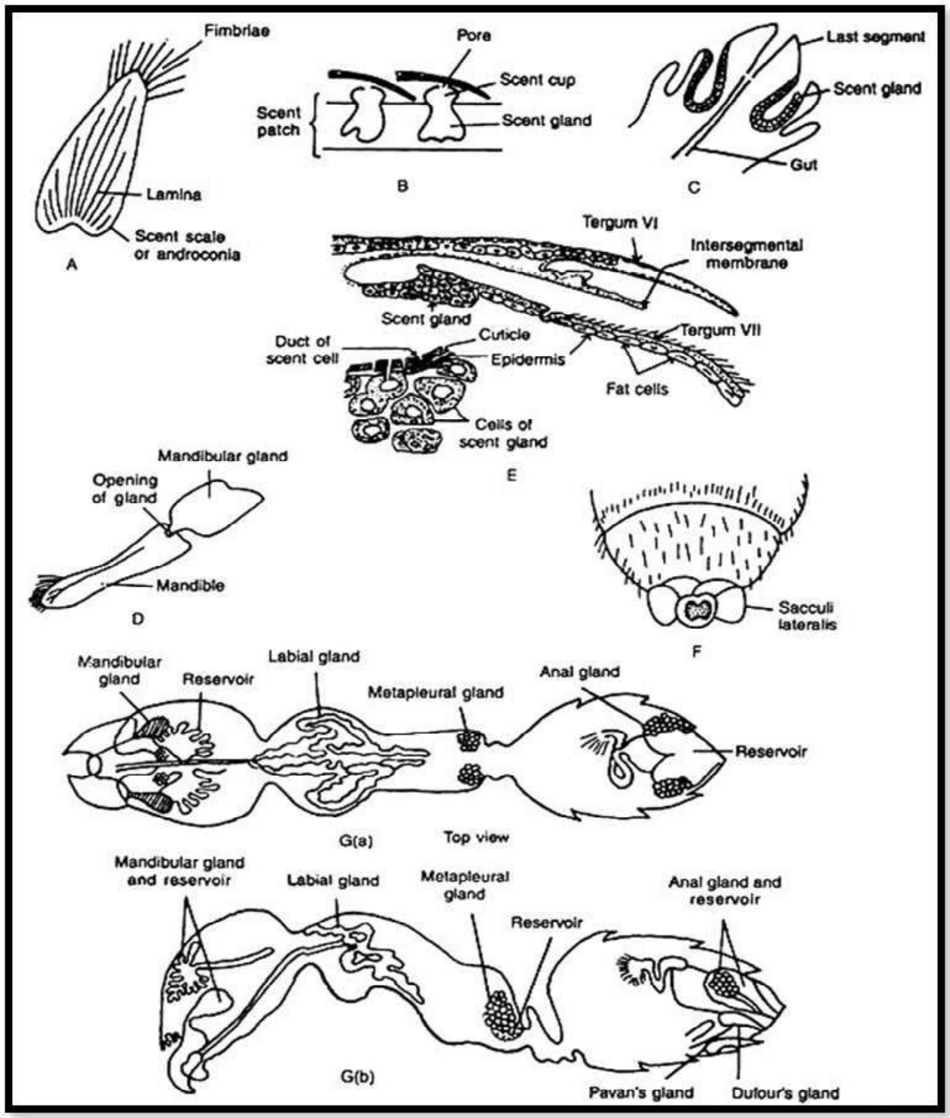


Fig. 3.4 *Pheromones Producing Glands in Insects*

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 pre-sent 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 struc-tures called scent cups. 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 invaginted glands which open on either sides of the last abdominal segment. By evagination of this gland, scent is dis-persed. Female silk moth emits a sex pheromone called bombykol from a pair of sacs called sacculi lateralis. It is found on the last abdominal segment.

iii. In Hymenoptera

a. **Honey Bee:** In honey bee pheromones are liberated from two glands, i.e., mandibular and Nassanoff's glands:

- **Mandibular Gland:** Mandi-bular glands are located in the head region. It is a sac-like structure and their duct opens at the base of the mandible. They are well-developed in the queen and workers but reduced in drones.
- **Nassanoff's Gland:** Nassanoff's gland was discovered in 1882 by a Russian biologist, after whom it was named. It is found below the inter-segmental membrane (arthrodial mem-brane) 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.

b. **Ants:** Mainly pheromones control the social behaviour of ants as most of their signalling 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 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 pheromone 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 anten-nae are sensing equal concentrations and thus guide the ants straight down the odour trail.

3.3.3 Functions of Pheromones

Pheromones serve a number of functions in invertebrates, i.e., as follows:

A. Sex Attractants: Pheromones are employed by various animals to attract the other sex for mating.

i. Pheromones of Females

Female insects usually release pheromones by exposing the concerned glands. Generally, they are released at particular time of the day, depending upon the diurnal or nocturnal nature of the animal. The scent thus released excites the approaching male and serves as a guide for reaching the female.

The queen bee attracts drone by releasing pheromones from two glands, i.e., mandibular and Nassanoff's. The secretion of phero-mones from these two glands serves her to rule over a colony of 6,000-8,000 individuals for a period of 5 to 7 years. The male Emperor moth (*Endia parvonia*) can detect the sex attractant of the female as far as 13 kms, although the female carries less than 0-001 part of a milligram.

ii. Pheromones of Males

Very few instances of male producing sex-attractant is present in the animal world. The male beetle, (*Harpobittacus*) from its posterior abdominal segments, releases a scent which excites female for mating. This it does while feeding upon a prey. When the female arrives, the male presents her with the remainder of the prey. While the female is busy eating, the male beetle copulates with her.

B. Communication in Social Insects

Many ant species create smell trails to help them navigate. Pheromones have a function in communication among fire ants. After finding a food source, the worker returns to the nest by leaving a trail.

When a forager ant comes across a coworker, it hurries over to it and tries to alert it to the trail substance. Initially, the trail consists of a series of scent spots left by the forager ant as it returns to its nest by contacting the ground with its abdomen.

Sub-sequently, as more worker ants enter the fray, the spots they all create may eventually merge into a continuous path. The trail of the fire ants is formed by substances secreted in minute amount from Dufour's gland present in the abdominal edge.

The trail is not only used for leading to the food, but may be used for other purposes, such as for routine pas-sage or for emergency exit. Sometimes alarm pheromones from mandibular or anal gland attract other mem-bers of the colony, who come to its rescue.

In social insects the alarm pheromones perform three main functions:

- To alert the colony.
- To release aggression.
- To mark the target to be attacked.

Pheromones are volatile. Pheromones used for marking trails or territory are less volatile, while distress pheromones are high-ly volatile. If one is stung by a bee and if by reflex the bee is killed, then the stinging of dead bee may release alarm and distress pheromones, which triggers a mass attack from the hive.

Worker honey bees are attracted towards each other by scent from Nassanoff's gland.

The scent from Nassanoff's gland may be released in various situations, such as:

- At the time of feeding.
- During formation of new hive.
- To mark a source of water.
- To mark hive for recognition.
- For maintaining cohesion of swarm during flight.

C. Maintenance of Social Structure

i. The queen bee produces phero-mones which help in controlling the social structure of her colony. If the queen is removed or dies then the workers become restless and start building emergency queen cells or royal chambers. The larvae within these cells are fed with Royal jelly.

The queen which emerges first, stings the remaining sisters to death. However, in the presence of the queen, this behaviour of the workers of building new royal chambers is kept under control by a pheromone produced by the mandibular gland.

ii. The queens of certain Vespine wasps, who live in smaller colonies, produce pheromones that maintain the stability of the colony.

iii. In termites the number of a parti-cular cast is regulated by a number of pheromones. In the absence of the queen, its replacement is produced within a week. In termites also more than one queen is produced. As soon as the first queen emerges, the rest of the developing queens are eaten up by the workers. Even when the old queen stops producing pheromones it is also eaten up by the workers.

D. Trapping Prey

Some insects use pheromones to trap the prey. For example, bolas spider tricks the male moths that are searching for mates. To attract the moths, the bolas spider secretes a scent that is similar to the scent secreted by the female moth. The male moth comes near to the scent and is eaten up by the spider.

E. For Pest Control

The species-specific quality of pheromones can be used to attract and capture designated target animals. For example, traps that contain the scent from female Japanese beetles can be used to attract males as a pest control procedure.

The use of pheromones to control phases of the lives of pest species is one method of pest management. Beet army-worms are a serious pest in cotton-producing areas of the United States, causing multi-million dollar losses in 1995 in Texas alone. In 1997, researchers reported success in disrupting mating procedures between male and female Beet army-worms by flooding 35-acre cotton field plots with sex attractant pheromones. With such a pervasion of female scent, the males could not find females for more than 100 days. Certain pheromone traps have been developed and are in common usage by homeowners. Indian Meal Moths (Pantry moths) are attracted to a pheromone in a small box lined with a sticky substance and are thus captured for disposal.

F. Inhibitory Pheromones

Inhibitory pheromones inhibit the action of other pheromones produced by the same species. For example, Verbenone reduces the response of sex attractant pheromones of *Dendroctonus* (beetle). Thus, excessive aggregation of this species leading to overcrowding on the host plant is avoided.

Adverse Effects of Pheromones

Pheromones sometimes have certain adverse effect on the user:

- The pheromones produced by Anagasta larva induce the parasite, Venturia, to make probing movement with its ovipositor. This increases the larva getting parasitized.
- Pheromones sometimes advertise the presence of an insect predator and potential parasite. The Cleridae beetle (*Thanasimus dubius*) is a predator of Dendroctonus (beetle). It thus is able to locate its host by responding to the pheromone frontalin secreted by the host.

Check Your Progress

5. Why is communication essential in animals?
6. What are pheromones?
7. How do pheromones differ from visual or auditory cues?
8. How were pheromones discovered?
9. What type of nature does pheromones possess?
10. Name any four types of pheromones.
11. How aggregation pheromones are produced?
12. How are epideictic pheromones different from territory pheromones?

3.4 NERVOUS INTEGRATION: LEARNING AND MEMORY

Let us now discuss nervous system in insects.

Nervous System in Insects

The nervous system of an insect is a network of specialized cells also called as neurons that act as an internal 'information highway'. Electrical impulses, i.e., action potentials are generated by these cells and pass over the cell membrane as depolarization waves. The action potential is propagated by filament-like processes (dendrites, axons, or collaterals) in each neuron. Signal transmission is always unidirectional, with dendrites or collaterals pointing toward the nerve cell body and axons pointing away from it.

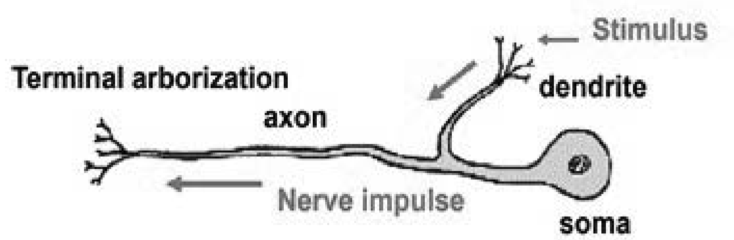
Neurons are usually divided into three categories, depending on their function within the nervous system as following (Refer Figure 3.5):

- **Afferent or Sensory Neurons:** These are bipolar or multipolar cells have dendrites that are associated with sense organs or receptors. They always carry information toward the central nervous system.
- **Efferent or Motor Neurons:** Unipolar cells that conduct signals away from the central nervous system and stimulate responses in muscles and glands.

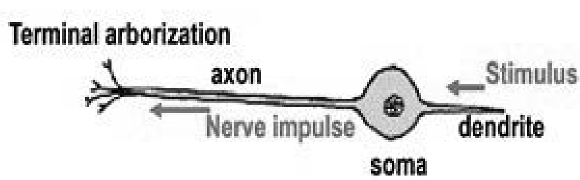
- **Internuncial or Association Neurons:** Unipolar cells (often with several collaterals and/or branching axons) that conduct signals within the central nervous system.

Individual nerve cells connect with one another through special junctions, called synapses. When a nerve impulse reaches the synapse, it releases a chemical messenger (neurotransmitter substance) that diffuses across the synapse and triggers a new impulse in the dendrite(s) of one or more connecting neurons. Acetylcholine, 5-hydroxytryptamine, dopamine, and noradrenaline are examples of neurotransmitters found in both vertebrate and invertebrate nervous systems.

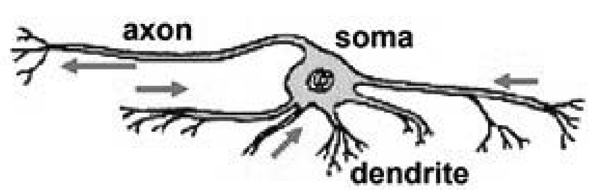
Nerve cells are typically found grouped in bundles. A nerve is simply a bundle of dendrites or axons that serve the same part of the body. A ganglion is a dense cluster of interconnected neurons that process sensory information or control motor outputs.



Unipolar Neuron



Bipolar Neuron



Multipolar Neuron

Fig. 3.5 *Different Types of Neurons*

The Central Nervous System (CNS)

Insects have a very simple Central Nervous System (CNS), with a dorsal brain connected to a ventral nerve cord made up of paired segmental ganglia running along the ventral midline of the thorax and abdomen, similar to most other arthropods. A short medial nerve (commissure) connects the ganglia in each segment, while intersegmental connectives connect the ganglia in adjacent body segments.

The Central Nervous System (CNS) resembles a ladder in appearance, with commissures serving as the rungs and intersegmental connectives serving as the rails. In more advanced insect orders there is a tendency for individual ganglia to combine (both laterally and longitudinally) into larger ganglia that serve multiple body segments.

An insect's brain is a complex of six fused ganglia (three pairs) located dorsally within the head capsule. Each part of the brain controls (innervates) a limited spectrum of activities in the insect's body:

- **Protocerebrum:** Protocerebrum is the first pair of ganglia are largely associated with vision; they innervate the compound eyes and ocelli.
- **Deutocerebrum:** Deutocerebrum is a second pair of ganglia process sensory information collected by the antennae.
- **Tritocerebrum:** Tritocerebrum is the third pair of ganglia innervate the labrum and integrate sensory inputs from proto- and deutocerebrum. They also link the brain with the rest of the ventral nerve cord and the stomodaeal nervous system that controls the internal organs. The commissure for the tritocerebrum loops around the digestive system, suggesting that these ganglia were originally located behind the mouth and migrated forward (around the esophagus) during evolution.

Another cluster of fused ganglia is located ventrally in the head capsule (just below the brain and oesophagus) (jointly called the subesophageal ganglion). This structure is thought to contain neural elements from the three primordial body segments that united with the head to form mouthparts, according to embryologists. The hypopharynx, salivary glands, and neck muscles are all innervated by the subesophageal ganglion in modern insects, in addition to the mandibles, maxillae, and labium. The brain and subesophageal complex are linked by a pair of circumesophageal connectives that loop around the digestive tract.

Three pairs of thoracic ganglia (which are sometimes merged) govern locomotion in the thorax by innervating the legs and wings. These ganglia are also linked to thoracic muscles and sensory receptors. Abdominal ganglia control abdominal muscle movements in a similar way. A pair of lateral nerves that emerge from each segmental ganglion control spiracles in the thorax and abdomen (or by a median ventral nerve that branches to each side). The anus, internal and external genitalia, and sense receptors (such as cerci) on the insect's back end are all innervated by a pair of terminal abdominal ganglia (which are frequently merged to form a massive caudal ganglion) (Refer Figure 3.6).

The Peripheral Nervous System (PNS) consists of all of the motor neuron axons that radiate to the muscles from the ganglia of the CNS and stomodeal nervous system plus the sensory neurons of the cuticular sensory structures (the sense organs) that receive mechanical, chemical, thermal, or visual stimuli from an insect's environment.

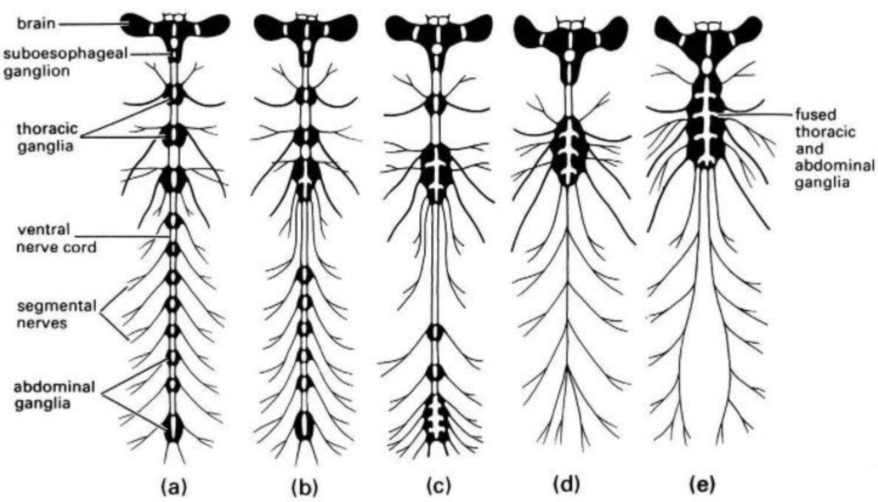


Fig. 3.6 *The Central Nervous System of Various Insects Showing the Diversity of Arrangement of Ganglia in the Ventral Nerve Cord*

The above Figure 3.6 illustrates the varying degrees of fusion of ganglia occur from the least to the most specialized, in which A. shows three separate thoracic and eight abdominal ganglia, as in *Dictyopterus* (Coleoptera: Lycidae) and *Pulex* (Siphonaptera: Pulicidae); B. shows three thoracic and six abdominal, as in *Blatta* (Blattodea: Blattidae) and *Chironomus* (Diptera: Chironomidae), C. shows two thoracic and considerable abdominal fusion of ganglia, as in *Crabro* and *Eucera* (Hymenoptera: Crabronidae and Anthophoridae), D. shows highly fused with one thoracic and no abdominal ganglia, as in *Musca* , *Calliphora*, and *Lucilia* (Diptera: Muscidae and Calliphoridae); and E. shows extreme fusion with no separate suboesophageal ganglion, as in *Hydrometra* (Hemiptera: Hydrometridae) and *Rhizotrogus* (Scarabaeidae).

The Stomodaeal Nervous System

A stomodaeal (or stomatogastric) nerve system innervates the majority of an insect's internal organs. The brain is connected to a frontal ganglion (unpaired) on the anterior wall of the oesophagus by a pair of frontal nerves that emerge around the base of the tritocerebrum. The throat and muscles involved in swallowing are innervated by this ganglion. The frontal ganglion is connected to a hypocerebral ganglion that innervates the heart, corpora cardiaca, and sections of the foregut by a recurrent nerve that runs along the anterio-dorsal surface of the foregut. The hypocerebral ganglion sends gastric nerves to the ingluvial ganglia (paired) in the abdomen, which innervate the hind intestine (Refer Figure 3.7).

In comparison to vertebrates, an insect's nervous system is far more de-centralized. Most overt behaviour, for example feeding, locomotion, mating, etc. is integrated and controlled by segmental ganglia instead of the brain. In some cases, the brain may stimulate or inhibit activity in segmental ganglia but these signals are not essential for survival. Indeed, a headless insect may survive for days or weeks (until it dies of starvation or dehydration) as long as the neck is sealed to prevent loss of blood.

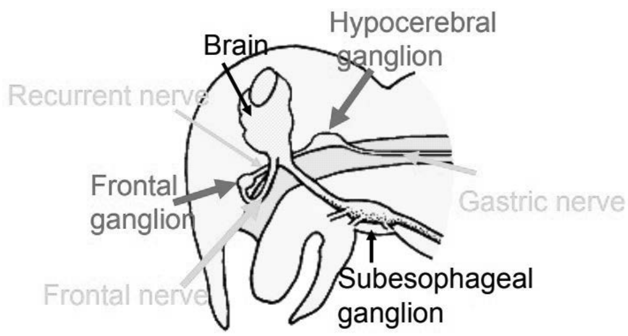


Fig. 3.*7 Stomodaeal Nervous System*

Insects possess miniature brains but exhibit a sophisticated behavioural repertoire. Recent studies have reported the existence of unsuspected cognitive capabilities in various insect species that go beyond the traditionally studied framework of simple associative learning. Animals constantly monitor both their internal and their external environment and make the necessary adjustments in order to maintain themselves optimally and thus to develop and reproduce at the maximum rate. The adjustments they make may be immediate and obvious, for example flight from predators, or longer-term, for example entry into diapause to avoid impending adverse con-ditions. The nature of the response depends, obviously on the nature of the stimulus. A stimulus rarely acts directly on the effector system; instead, it is usually always received by an appropriate sensory structure and sent to the central nervous system, which determines an appropriate response in the given conditions. The nerve system transmits the message to the effector system when a reaction is immediate, that is, achieved in a couple of seconds or less. Such reactions are usually just transitory. Chemical communications, i.e., hormones are used to induce delayed reactions, which are often longer-lasting. An individual's neurological and endocrine systems are the systems that coordinate the response with the stimulus. Pheromones, which constitute another chemical regulating system, coordinate the behaviour and development of a group of individuals of the same species.

Learning in Insects

Learning is a cognitive process in which one's behaviour changes as a result of an experience. It is worth noting that many behaviour that necessitate complicated computations are, despite the use of learnt input parameters, intrinsic mechanisms. The brain mechanisms used by ants in a path integration orientation system, for example require the computation of a homing vector from hundreds of individual direction and distance (measurements). Honey bees (*Apis mellifera*) can calculate the azimuth of the sun even when they have not seen it in hours and do not have to learn how to do so. Successive generations of monarch butterflies navigate from Mexico to North America and back without prior experience. The ability to perform certain, even complex, computations can thus be hardwired and heritable. However, many behaviours exhibited by insects involve learning, particularly in the contexts of orientation, choice of food sources, and other task performance. Most research on insect cognition to date has been conducted on a few model organisms, such as Drosophila and the honey bee. Because the neurobiology and genetics of these model organisms are studied intensively, this enables researchers to investigate the relationship between cognition and the neurological circuitry in great detail.

Learning Biases

Through learning, insects can increase their foraging efficiency, decreasing the time spent searching for food which allows for more time and energy to invest in other fitness related activities, such as searching for mates. Depending on the ecology of the insect certain cues may be used to learn to quickly identify food sources. Over evolutionary time insects may develop evolved learning biases that reflect the food source they feed on. Biases in learning allow insects to quickly associate relevant features of the environment that are related to food. For example, bees have an unlearned preference for radiating and symmetric patterns-features of natural flowers bees forage on. Additionally, bees that have no foraging experience tend to have an unlearned preference for the colours that an experienced forager would learn faster. These colours tend to be those of highly rewarding flowers in that particular environment.

Time-Place Learning

In addition to more typical cues like color and odor, insects are able to use time as a foraging cue. Time is a particularly important cue for pollinators. Pollinators forage on flowers which tend to vary predictably in time and space, depending on the flower species, pollinators can learn the timing of blooming of flower species to develop more efficient foraging routes. Bees learn at which times and in which areas sites are rewarding and change their preference for particular sites based on the time of day. These time-based preferences have been shown to be tied to a circadian clock in some insects. In the absence of external cues honeybees will still show a shift in preference for a reward depending on time strongly implicating an internal time-keeping mechanism, i.e., the circadian clock, in modulating the learned preference. Moreover, not only can bees remember when a particular site is rewarding but they can also remember at what times multiple different sites are profitable. Certain butterfly species also show evidence for time-place learning due to their trap-line foraging behaviour. This is when an animal consistently visits the same foraging sites in a sequential manner across multiple days and is thought to be suggestive of a time-place learning ability.

Innovation Capacity

Insects are also capable of behavioural innovations. Innovation is defined as the creation of a new or modified learned behaviour not previously found in the population. Innovative abilities can be experimentally studied in insects through the use of problem solving tasks. When presented with a string-pulling task, many bumblebees cannot solve the task, but a few can innovate the solution. Those that initially could not solve the task can learn to solve it by observing an innovator bee solving the task. These learned behaviors can then spread culturally through bee populations. More recent studies in insects have begun to look at what traits (for example, exploratory tendency) predict the propensity for an individual insect to be an innovator.

Check Your Progress

13. In how many categories neurons are divided?
14. Define the term synapses.

3.5 DIAPAUSE IN INSECTS

Diapause is a developmental pause that has the effect of facilitating survival in unfavorable conditions, but it is not immediately linked to the unfavorable environment. It is characterised as a physiological state of dormancy or developmental halt in which most life functions are shut down. This is a survival adaptation that is typically seen in arthropods.

In temperate climates, diapause is primarily concerned with surviving through the cold winter months when normal growth is impossible. However, in the tropics, it may help with survival during the dry season, which is marked by a lack of moisture and food. Diapause is triggered by unfavourable conditions, such as heat, cold, or harsh environmental conditions and it is a natural response of insects to protect themselves from these conditions. Diapause in insects is mainly caused by adverse conditions, such as a lack of food, variations in day length and temperature, and so on. During the diapause of insects, concentration of growth hormones starts decreasing and thus slow down the process of development.

This can happen at any point during an insect's life cycle (from its pupae stage to the active or adult stage). When this happens at the egg or pupil stage, for example in the pupae stage of insects like cocoons of moths, development slows to a halt. Insect feeding habits and reproductive behaviour slow down or stop in the adult stage. Many insects go through a diapause at different stages of their development, during which their development comes to a halt, metabolism is lowered to a bare minimum and the insect is completely insensitive to even the most unfavorable environmental conditions. In many animals, the impact of external influences on a critical stage of development affects whether or not diapause will occur. This sensitive period occurs well before the onset of diapause. It could have been a generation before in the instance of the silk moth. External variables have a greater or lesser impact on the termination of diapause in all cases. Unlike a halt in activity caused by unfavorable external conditions, which only ends when the favourable conditions return. Even the most unfavorable environmental factors, such as a period of cold, might cause diapause to terminate. There are numerous gradations between true diapause and the arrest of development under unfavorable conditions. The adults of many beetles, overwintering in the diapause state, show atrophy of their gonads and hypertrophy of the fat body. In *Anthonomus grandis* there is an increase in the water content and a decrease in fat content in early spring and this is followed by the beginning of spermiogenesis. The oogenesis takes place only after the female has taken food. In Colorado potato beetle (*Letinotarsa decemlineata*) the development of gonads begins at the end of diapause. So, even though diapause meaning indicates that it is a genetic phenomenon, it can be removed experimentally by providing favorable conditions to the animals.

Organisms that Exhibit Diapause

Prodoxus y-inversus is a moth that can sleep for up to 19 years. This is the longest diapause ever documented in biological research. This moth is found in Southwestern Mexico and the United States. Diapause is also seen in a few other animal species. Several arthropods, such as the Southwestern corn borer, tobacco hornworm, and meat fly, go through embryological diapause. Between the late larval and late embryonic stages of the silkworm, there are diapauses. Diapause is seen in a variety of mites and insects, as well as a few snails and crustaceans. Mummichog is a small killfish that goes dormant during its embryonic stage.

Types of Diapause

Diapause can be either obligatory or facultative:

- **Obligatory Diapause**: In obligatory diapause every individual in every generation enters diapause. Obligatory diapause is most often associated with univoltine insects, which means insects having one generation per year.
- **Facultative Diapause**: In some species of insects, some generations may be completely free of diapause while in other generations some or all of the insects may enter diapause. Insects with facultative diapause undergo a period of suspended development only when conditions require it for survival. Facultative diapause is found in most insects and is associated with bivoltine (having two generations per year) or multivoltine insects (more than two generations per year).

Additionally, some insects undergo reproductive diapause, which is a suspension of reproductive functions in adult insects. The best example of reproductive diapause is the monarch butterfly in North America.

Stages of Diapause (Harsimran *et al*., 2017)

Diapause is a dynamic process which is consisting of several successive phases (Refer Figure 3.8).

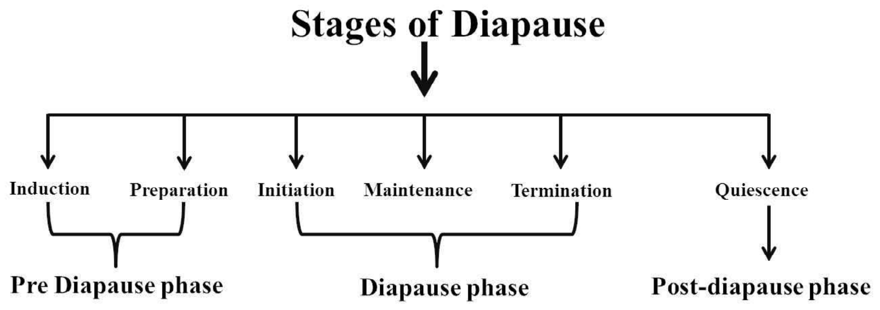


Fig. 3.8 *Stages of Diapause*

Pre Diapause Phase

- **Induction:** Induction occurs much before the onset of unfavourable environmental conditions. Essentially, certain environmental stimuli, called token stimuli triggers the diapause behaviour. The stimuli themselves do not negatively affect any of the factors, though they signify an impending transformation in the environmental conditions.

- **Preparation:** The induction phase is followed by the preparation phase. In this phase, the behavioural and physiological preparations for diapause may take place. Basically, the insects start preparing itself, such as storing molecules like carbohydrates, proteins and lipids to sustain themselves during the diapause. For example diapause in puparia of flesh fly increases the amount of cuticular hydrocarbons lining the puparium which effectively reducing the ability of water to cross the cuticle.

Diapause Phase

- **Initiation:** Initiation is the most important stage of diapause. The initiation stage is characterized by cessation of morphological development, which is commonly followed by regulated metabolic suppression. Mobile diapause stages may continue accepting food, building of energy reserves and seeking suitable microhabitat. Physiological preparations for the period of adversity may take place and intensity of diapause may increase. These include a change in colour, moulting into a diapause stage or release of special enzymes.

  Adults of fire bug, *Pyrrhocoris apterus*, have the enzymatic complement that allows them to accumulate polyhydric alcohols, molecules that help to lower their freezing points and thus preventing them during freezing.

- **Maintenance:** Maintenance is characterized by the reduced metabolism and arrest of embryological development. Specific token stimuli may help to maintain diapause (prevent its termination). Metabolic rate is relatively low and constant. Furthermore, sensitivity to certain stimuli is increased, especially the ones that prevent the termination of the diapause is decreased.

- **Termination:** Termination, as the name implies, terminates the diapause. By the end of the termination phase, a physiological state is reached, in which direct development may overtly resume. However, certain insects rely on specific environmental stimuli to trigger the termination of diapause.

The end of diapause is brought about in different insects of different ways. In Lepidoptera it is ended by the previous action of cold, so that the brain influences the prothoracic glands. It is, therefore, the action of prothoracic glands hormone, which terminates diapause. The adult diapause of *Leptinotarsa decemlineata* is broken by the gonadotrophic hormone of the corpora allata. The egg diapause of the Grasshopper *Melanoplus* is broken by the removal of the waxy-layer cover, thus permitting the penetration of water through the micropyle. The egg diapause of the Mosquito *Aedeshex odontus* is not ended by absorption of water and not also be changes of the photoperiod but only by cold treatment. The egg diapause of the grasshopper *Acheta commodus* is also broken by the action of cold. It is, therefore, evident that not only the external factors but also the physiological mechanism is important in breaking diapause.

Post-Diapause Phase

- **Quiescence:** During Post-diapause quiescence, inhibition of development and metabolism was exogenously enforced, which follows the termination of diapause when conditions are not favorable for resumption of direct development. It implies reorganization prior to full activity. Termination is followed by the state of quiescence, where the insect can resume development, provided the environmental conditions become quite favourable.

There are numerous external and internal factors that regulating the diapause in insects at several levels: Environmental stimuli interact with genetic pre-programming to affect neuronal signalling, endocrine pathways, and, eventually, metabolic and enzymatic changes (Refer Figure 3.9).

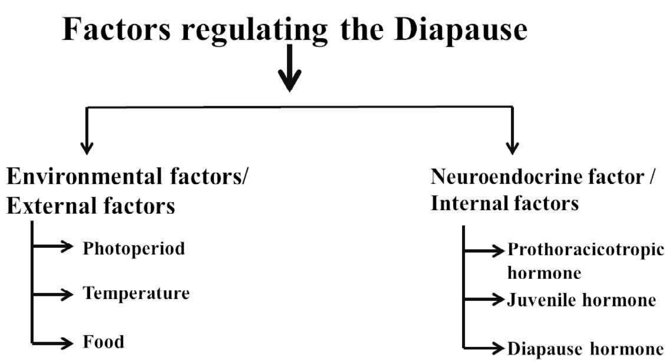


Fig. 3.9 *Factors Regulating the Diapause*

Environmental Factors (External)

Diapause in insects is induced or terminated in response to environmental cues. These cues may include changes in the length of daylight, temperature, food quality and availability, moisture, pH, and other factors. No single cue solely determines the start or end of diapause. Their combined influence, along with programmed genetic factors, controls diapause.

- **Photoperiod:** A photoperiod is the alternating phases of light and dark in the day. Seasonal changes to the photoperiod, such as shorter days as winter approaches cue the start or end of diapause for many insects. Photoperiod is the most important.
- **Temperature:** Along with photoperiod, changes in temperature, such as an extreme cold spell can influence the start or end of diapause. The thermo period, alternating phases of cooler and warmer temperatures, also influences diapause. Some insects require specific thermal cues to end the diapause phase. For example, the woolly bear caterpillar must endure a period of chilling to trigger the end of diapause and continuation of the life cycle.
- **Food:** As the growing season ends, the diminishing quality of their food sources may help trigger a diapause phase in an insect species. As potato plants and other hosts turn brown and dry, for example Colorado potato beetle adults enter a state of diapause.

Neuroendocrine Factor (Internal)

The neuroendocrine system of insects consists primarily of neurosecretory cells in the brain, such as corpora cardiaca, corpora allata and the prothoracic glands. There are several key hormones involved in the regulation of diapause: Prothoracicotropic Hormone (PTTH), Juvenile Hormone (JH) and Diapause Hormone (DH).

- **Prothoracicotropic Hormone**: Prothoracicotropic hormone stimulates the prothoracic glands to produce ecdysteroids that are required to promote development. Diapause in larval and pupa are regulated by an interruption of this connection, either by preventing release of prothoracicotropic hormone from the brain or by failure of the prothoracic glands to respond to Prothoracicotropic Hormone (PTTH).
- **Juvenile Hormone (JH):** The corpora allata is responsible for the production of Juvenile Hormone (JH). In the Bean bug, *Riptortus pedestris*, clusters of neurons on the protocerebrum called the pars lateralis maintain reproductive diapause by inhibiting JH production by the corpora allata. Adult diapause is often associated with the absence of Juvenile Hormone (JH), while larval diapause is often associated with its presence. In adults, absence of JH causes degeneration of flight muscles and atrophy or cessation of development of reproductive tissues, and halts mating behaviour. The presence of JH in larvae may prevent moulting to the next larval instar, though successive stationary moults may still occur. In the Corn borer, *Diatraea gradiosella*, JH is required for the accumulation by the fat body of a storage protein that is associated with diapause.
- **Diapause Hormone (DH):** Diapause Hormone (DH) regulates embryonic diapause in the eggs of the Silkworm moth, *Bombyx mori*. Diapause Hormone (DH) is released from the subesophageal ganglion of the mother and triggers trehalase production by the ovaries. This generates high levels of glycogen in the eggs, which is converted into the polyhydric alcohols glycerol and sorbitol. Sorbitol directly inhibits the development of the embryos. Glycerol and sorbitol are reconverted into glycogen at the termination of diapause.

Control of Diapause

Diapause is caused by a lack of ecdysone, which prevents growth and moulting in larvae and pupae, as well as possibly in late embryonic stages. The absence of the corpus allatum hormone causes the oocytes to fail to mature during adult diapause. The neurosecretory cells of the brain control the action of both the prothoracic gland and the corpora allata, and their failure to function during diapause is due to their inactivity.

Diapause in eggs that are just starting to mature must be mediated by a separate mechanism because they lack an endocrine system at this stage. Diapause is induced in Bombyx eggs by a diapause-inducing hormone released by the parent's neurosecretory cells in the suboesophageal ganglia. In addition, the maternal corpora allata secretes an antagonistic hormone that blocks the diapause-inducing hormone. The brain controls the release of two secretions, and changes in the balance of the two hormones are responsible for the variances across Bombyx races.

Check Your Progress

15. Define the term diapause.
16. Write about different types of diapause.
17. What is termination in diapause?
18. What does control of diapause mean?

3.6 MIMICRY IN INSECTS

Mimicry is the superficial but striking likeness in form, colour, attitude, and activity of one creature to another or to inanimate objects. This aids the organism in a variety of ways, including concealment, defense, and other benefits. The word mimicry comes from the Latin word mimicus, which means imitation or simulation. The organism that mimics is known as a **mimic**, while the organism that copies is known as a **model**. The advantage is one-sided in the most well-studied mimetic partnerships, with one species (the mimic) benefiting from a likeness to the other (the model). Many plants and animals have been discovered to be mimetic since the discovery of mimicry in butterflies in the mid-nineteenth century. In many cases the organisms involved belong to the same class, order, or even family, but numerous instances are known of plants mimicking animals and vice versa. Although the best-known examples of mimicry involve similarity of appearance, investigations have disclosed fascinating cases in which the resemblance involves sound, smell, behaviour and even biochemistry.

Types of Mimicry

Mimicry can broadly be classified into following types:

- Protective Mimicry (Concealing Mimicry, Warning Mimicry)
- Aggressive Mimicry (Concealing Mimicry, Alluring Mimicry)
- Warning Mimicry
- Aggressive Mimicry
- Batesian Mimicry
- Mullerian Mimicry
- Automimicry
- Conscious Mimicry

Protective Mimicry: Protective mimicry includes imitation of organism to other organisms or surrounding in form of colour or behaviour. It is protective in function. This could be obtained either by concealment or by warning.

Concealing Mimicry: Protective mimicry is a common occurrence. The organisms blend in with their surroundings by changing their coloration. They can imitate the shape and colour of other organisms or objects in some situations. Cryptolithodes is a white crab with a smooth, spherical shape. It blends in wonderfully with the beach's white quartz pebbles. Geometrid moth *Selenia tetralunaria* caterpillars look like birch tree twigs and smaller branches. By grabbing the branch with its two hind pairs of prolegs and throwing its body outward at an angle, the caterpillar avoids being seen by predators. Because of their narrow bodies, shortened limbs, and sympathetic coloration, many walking-stick insects resemble twigs. The most perfect example is the leaf insect Phyllium. It possesses flattened and expanded body and limbs. It is green in colour except for irregular small yellowish spots which resemble the fungus or rust growth upon a leaf.

Indian dead-leaf butterfly, *Kallima paralekta* is the best example of protective mimicry. Its wings are strikingly coloured above with a reddish yellow or bluish white band. When the butterfly sits down, wings are folded with the upper surface together.

Warning Mimicry: Non-poisonous and harmless organisms imitate dangerous and hazardous creatures in this class. Similarly, the palatable variant looks and promotes as non-palatable. Many coral snakes in the Elapidae family have striking colours, with red and black stripes bordered by yellow. They have a potent venom, but because the gape is so small, they are safe to humans. Other species of innocuous snakes belonging to different genera of the Colubridae family imitate each of the toxic snake species. Heterodon, a non-poisonous hog-nose snake, has a flattened, triangular head. It frequently hiss and strike to show that it is very dangerous. The palatable Viceroy butterfly *Basilarchia archippus* which can be easily preyed upon, mimics the distasteful non-palatable Monarch butterfly *Anosia plexippus.*

Aggressive Mimicry: Aggressive mimicry is exhibited by certain carnivorous spiders, fishes and lizards. These animals remain unnoticed by matching with the surrounding. On the approach of prey, they pounce over and kill them. Spiders are the typical examples. In most cases the yellow body harmonies so perfectly with the colour of the flower upon which they rest that they become invisible for the visiting insects which constitute the spider's prey.

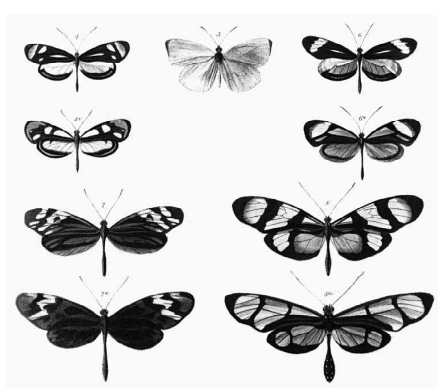
- **Concealing Mimicry:** In concealing mimicry animals develop cryptic colours and blend with surrounding. Spiders resemble in space and colour to the flowers on which they live. These predators are not easily distinguished from the flowers.
- **Alluring Mimicry:** In alluring mimicry type the predator possesses some attraction to appeal its prey. The deceive prey become a victim. Certain spiders mimic the flowers of orchid and insects are attracted to collect honey. Deep sea Angler fish *Lophius* has first ray of dorsal fin modified to illicium and it works as bait.

Batesian Mimicry: The edible species deceptively similar colour patterns would give protection from the same predators. Batesian mimicry is named after its discoverer, and it occurs when a vulnerable creature shows a striking likeness to a toxic and visible one. If it resembles a warningly coloured inedible species, a reasonably pleasant species gains an advantage from predators. This false warning coloration is known as Batesian type warning mimicry. Bates came to the conclusion that the inedible species distinct hue served as a warning to predators who had learnt of their inedibility through experience (Refer Figure 3.10).

Mullerian Mimicry: If two of unpalatable species resemble each other, is called Mullerian mimicry. Mullerian mimicry is advantageous for both but Batesian mimicry is good only to the edible species (Refer Figure 3.10).

Mullerian mimicry is a natural phenomenon in which two or more well-defended species, often foul-tasting and that share common predators, have come to mimic each other's honest warning signals, to their mutual benefit. This works because predators can learn to avoid all of them with fewer experiences with members of any one of the relevant species. In 1878 Fritz Muller, a German zoologist, suggested that an explanation that the predator has learned to avoid the particular colour pattern with which it had its initial contact, it would then avoid all other similarly patterned species, edible and inedible. The initial learning experience of the predator often results in death or damage to the inedible individual that provided the lesson; there is thus some cost to the species that teaches the predator of its inedibility. The tendency of inedible or noxious species to resemble each other is called Mullerian mimicry.

A. Mullerian mimicry (source-internet)



B. Batesian mimicry (source-internet)

Fig. 3.10 *Types of Mimicry A. Mullerian Mimicry; and B. Batesian Mimicry*

Automimicry: The phenomenon of automimicry refers to how certain members of a species benefit from their likeness to other members of the same species. Although defenseless, males of many bees and wasps are protected from predators by their similarity to females with stingers. Some butterflies can protect themselves from predators by absorbing, tolerating, and retaining toxins from the plants they feed on while still juvenile (larval). Individuals or even subpopulations of such butterflies may not acquire such protection as a result of feeding on nonpoisonous plants, but predators that have sampled protected individuals of the savannah butterfly will avoid them.

Conscious Mimicry: Certain animals exhibit conscious imitation and on approach of danger behave as they are dead bodies. American opossum (*Didelphis virginiana*) becomes unconscious and simulates as dead. Many hard bodied beetles fall down like pebbles, when they are about to be seized by the enemy. For the enemy it is difficult to locate them among leaves and grass beneath.

Check Your Progress

19. Define the term mimicry.
20. Distinguish between mimic and model.
21. What makes concealing mimicry different from alluring mimicry?
22. What is mullerian mimicry?
23. Define the term automimicry.

3.7 INSECT BEHAVIOUR: SOCIAL LIFE, SYMBIOSIS AND ADAPTATIONS

An insect behaviour refers to the various actions of an insect in response to a stimulus or to its environment. It covers a wide range of activities, such as feeding, locomotion, grooming, reproduction, learning, migration, and communication.

Some insect behaviours are driven by the effects of the pheromones. Insects release chemicals that affect the behaviour of the other members of the same species as the latter perceive the released pheromones. When you see ants walking in a line and following one another they are really following a trail of pheromones that each one is leaving behind to show where to go. Most of these trails are by ants that are searching for food as they make their way back to the nest.

There are also insect behaviors that are influenced by environmental cues. Temperature, humidity, and toxins are some of the common environmental factors affecting insect behavior. Moths, for instance, show positive phototaxis, as they tend to fly towards the source of light.

Types of Insects Behaviour

In general, there are two types of behaviour observed in animals, i.e., innate behaviour and learned behaviour. The innate behaviour is one that is inherent or instinctive. It is genetically wired to the organism. This is exemplified by the behaviours associated with the dorsal light reaction. Moths tend to fly towards the source of light. The explanation for the moth's behaviour is still unclear. One possible reason is the instinctive tendency of the moth to keep the sun (light source) overhead or on its dorsal side. This is probably helping the moth to stay parallel to the ground.

Learned behaviour is a type of behaviour that the animal acquires through experience or learning. In insects, this learned behaviour is exemplified by insects foraging for food. Honey bees, for instance, are able to learn from environmental signals to locate the food source.

3.7.1 Social Life of Insect

Few animals belonging to the order Isoptera and Hymenoptera of class Insecta, display the phenomenon of social behaviour. These animals live in complex societies and are referred to as eusocial.

Eusociality

It is an extreme form of social behaviour found in just a few types of animals and is characterized by the following:

- Occurrence of polymorphic forms each assigned with a different function.
- Worker members of the colony provide food and care to the reproductive member and the early developmental stages of the colony.
- Division of labour in the colonies.
- The presence of several generations in a single hive/nest at the same time.

Social Insect: The term social insect generally refers to any of numerous species of insects that live in colonies and exhibit three characteristics namely group integration, division of labour and overlap of generations. In insects social life has evolved only in two orders, namely, Isoptera (termites) and Hymenoptera (bees, wasps and ants) which make a nest and live in colonies of thousands of individuals that practice division of labour and social interaction.

Bees

In the spring and throughout the honey flow period, a healthy bee hive's population can range from 40,000 to 80,000 individuals, but during the winter and extreme summer, the number drops. The hive is remarkably orderly, and there are no apparent disagreements among the members. The queen is 1.5 times the size of the workers and the sole reproductive female in the hive. Queen material, a pheromone secreted by the colony's mandibular glands, keeps the colony together. After emergence, young queens in multi-queen colonies strive to sting and kill competitor queens. Only one queen usually stays in the hive, while the rest of the queens, along with their army of workers, swarm out to find new areas to start their own hive. Queen takes one to several nuptial flights and after mating with drones settles in the hive and starts laying eggs. Drones are haploid fertile males of the colony, whose only job seems to be to mate with the queen and transfer their sperms in her spermatheca. There are 2-3 dozen drones in a bee hive all of which energetically pursue a queen in her nuptial flight. Once the breeding season is over drones are driven out of the hive by workers and die of starvation, since they are unable to forage for themselves. Workers in a hive are 20,000-80,000 in number, which are genetically sterile females that build, maintain and protect the hive. A worker attends to cleaning and maintaining the hive and feeding the larvae with honey and bee bread. It also secretes wax from the abdominal wax glands and participates in building honey comb cells. The workers function as foragers of nectar and pollen and in later part of life as water carriers, and eventually die while working.

In spring, a honeybee colony that grows sufficiently large splits in two, with the old queen and half her worker along with a daughter who will become a new queen make chambers in the ground in cliff, and in hollow tree. There are often many such sites within range of the waiting swarm, but only some motivate a worker to perform a dance back at the swarm a dance that communication information about the distance and quality of the potential new home. Other workers attend to a dancing scout and may be sufficiently stimulated to fully out to the spot themselves. If it is attractive to them they too will dance and send still more workers to the area then the swarm leaves its temporary perch and flies to the most popular nest site. The worker bees produce wax for the formation of the new hive and are known as builders. New hive is made hanging vertically from rock buildings or branches of trees consist of thousands of hexagonal chambers of cells made up of wax secreted by the builder's abdomen. The resins and gums secreted by plants are also used for construction and repair of the hive. The larvae are kept in the lower and central cells in the hive which are the 'Brood cells'. In Apisdorsata a brood cells are similar in shape and size but in other species brood cells are of three types viz worker cell for workers drone cells for drones and queen cell for the queen cell is used once only while rest are used a number of times there are no cells for lodging the adults. They generally keep moving about on the surface of the hive. The cells are mainly intended for the storage of honey and pollen especially in the upper portion of the comb. Colony of honeybees consists of three castes Queen, Drone and workers.

Caste Differentiation

Queen: Queen is the fertile female only that can lay up to 3000 eggs per day, which is twice the weight of her body but normal fecundity is about 600 eggs per day. The size of the queen is largest among other castes of bees Queen can be easily identified by its long abdomen strong legs and short wings. The queen has ovipositor on the tip of the abdomen It is the egg laying organ. The contribution of queen for its scullery is to lay eggs. Queen can produce male or female offspring. Unfertilized eggs develop into males and fertilized ones into females. Growing larvae, both of which are genetically females, can be developed into queens or workers by feeding them with royal jelly or pollen and honey by the workers. Queen produces a number of pheromones which attract workers and keeps the colony together. The secretions of mandibular glands, tergal and tarsal glands of queen are licked by the workers and passed to other members of the colony and larvae through food exchanges called trophallaxis. If a queen is killed, workers in the absence of queen pheromones, rear a new queen from the developing female larvae. Queen pheromone also inhibits development of ovaries in workers. Queen pheromone has stimulating effect on the activities of workers, such as comb building, brood rearing, foraging and honey making. If a queen dies or disappears, workers rear a new queen by selecting a larva and modifying its cell to make a queen cell and feed it exclusively with royal jelly.

Drone: Males members are called as drones, which are darker, robust and hairy and larger than workers. Drones are haploid fertile males the size of drone is smaller than queen but larger than sterile females, i.e., workers. They are developed from unfertilised eggs. There are about two dozen of them in a hive and chase the queen in air every time she ventures on nuptial flight. The secretions of mandibular glands and that of sting apparatus of queen attract drones during nuptial flight. They copulate with the queen and fertilize her eggs. Drones are not tolerated in the hive once the queen is fertilized and are generally driven out of hive, where they eventually die of starvation.

Workers: These are diploid sterile females and are smallest in size. They are sterile because of diet effect, queen substance and the pheromone. Their number in colony is the highest**.** The workers are genetically females but sterile as they are not fed on royal jelly in the larval stage. They have a lifespan of 6 weeks, the first half of which is spent in the hive attending to household chores, secreting wax and building hive, producing a highly nutritious royal jelly and converting nectar into honey. They become foragers in the later part of life and tirelessly collect nectar and pollen throughout life. They eventually die during performing their duties, an excellent example of honest and selfless service for the society. An amazing phenomenon that has been observed in honeybees is their capacity to reverse their age should a catastrophe struck the colony. In case of a crisis, such as destruction of the hive, the 4-5 week old foragers start reversing their age and become younger to secrete royal jelly and wax, repair their hive, rear anew queen from the larvae and rebuild their colony. Members of a colony are heavily dependent on one another and cannot survive in isolation, even if kept in the best of conditions. They communicate by ultrasound signals, pheromones, dancing and gestures. Workers possess numerous morphological adaptations to carry out their duties efficiently. Their mandibular glands secrete wax softening substance, pharyngeal glands secrete a gelatinous highly nutritious substance called royal jelly and stomach contains several glands that help in converting nectar into honey. There are wax glands on abdominal segments 4-7 which open by several ducts on to the sternites 4-7. Hind legs have tibia and basitarsus modified to form a pollen basket. Mouth parts of workers bees are of chewing and lapping type. Workers are sterile females and hence their ovipositors are modified in sting and accessory reproductive glands get modified to for alkaline and poison glands. A worker in its entire lifespan makes about a spoonful of honey. To make 500 grams of honey, bees have to extract nectar from more than 4 million flowers, for which they have to make about 50,000trips of the foraging area ranging between 5 km. In bee body the legs are modified and are hairy. When workers visit a garden of flower and sit on a flower pollen grains adhere to these hairs and other parts of the body Worker clean off pollen with the help of a special structure (the cleaners) present on each fore legs. Pollen brushes are present on every leg and pollen grains are stored in the pollen basket present on the outer surface of metatarsi on hind legs Nectar and water is collected in crop by sucking through mouth parts.

Worker bees possess Nabokov scent gland in their abdominal region which acts as a defensive organ and is modified ovipositor having a large poisonous storage sac and a sting. Poison storage sac contains a poisonous chemical. This chemical is injected into the body of enemy through sting. Worker bees attack collectively to the intruder and sting the intruder collectively. However, the tip of sting usually breaks into the body of intruder and the remaining secretion of alkaline gland mixed with that of poison gland (active poison) gets injected in her body thus it is killed by her own venom. Alarm and aggression pheromones are released by the worker bees from the abdomen by raising the tip of abdomen and protruding the sting apparatus (Refer Figure 3.11).

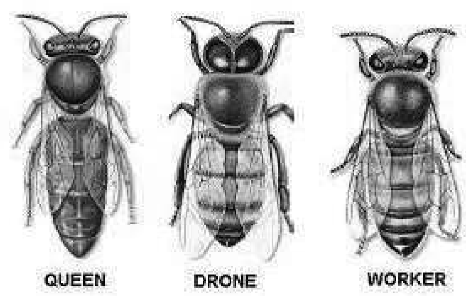


Fig. 3.11 *Caste Differentiation of Honey Bee*

Wasps

Insects known as wasps belong to family Vespidae, about 75,000 species of wasps are known, most of them parasitic or predators. Wasps are characterised by two pairs of membranous wings, three pairs of legs and an ovipositor that may be modified as sting in sterile females. The abdomen is narrowly attached to the thorax by a petiole. In addition to their compound eyes, wasps also have three simple eyes known as ocelli, arranged in a triangle on the top of the head. Females have diploid number of chromosomes and develop from fertilized eggs. Males are haploid and develop from unfertilized eggs. Yellow jackets and paper wasps prey on caterpillars and other larvae that can destroy crops. Wasps ingest floral nectar and help pollinate flowers. Wasps can be solitary or colonial, social insects that live in large colonies with thousands of members and build nests. Wasps build several types of nests depending on the species and region. Many social wasps build nests out of paper pulp in trees, holes in the ground, and other sheltered spots. Wasps, unlike honey bees, do not have wax glands. Instead, many people make paper out of wood pulp, which is collected locally from worn wood that has been softened by chewing and combining with saliva. The pulp is then utilised to build brood raising combs with cells. Mud daubers and pollen wasps construct mud cells in sheltered places typically on the sides of walls. Potter wasps similarly build vase-like nests from mud, often with multiple cells, attached to the twigs of trees or against walls.

Wasps cooperate together in nest building and brood care, and show some division of labour. But there is no morphologically differentiated queen. If workers get opportunity most, can become queens. Any female member of the colony can start a nest and bring up her offspring by herself without participating in social life. Thus wasps live in a primitive society. There are only two social aspects in context of social behaviour of wasps:

- The relationship between workers and grubs.
- The division of labour amongst their co-workers.

One Indian species of Wasps (*Polistes herbreus*) shows social behaviour. The adults are smaller and yellowish in colour. The most prominent Social wasp is

(*Vespa orientalis*). It is brownish and larger than yellow wasp. *Vespa niagnirica* is largest social wasp and it is dark brown in colour. Wasps prepare their nests over walls, ceilings, and trees near human habitats. Nests of French wasps (Polistes) and Indian wasps (Ropalidia) have some hexagonal chambers in which embryos are reared. Wasps remain active in summer and hibernate in winter. Through aggressive interactions the caste structure of the wasp's social system is maintained primarily among the colony members. If a queen fails to sustain 221 her dominant role, she will be replaced by another fertile female who assumes primary responsibility for egg production. Males develop only from unfertilized eggs which are usually laid by unmated workers. In tropical climates, social wasps are active throughout the year. New colonies often form by fission or swarming in which a fertile queen and a group of workers leave a large parent nest and set up housekeeping for themselves. In temperate climates, wasp colonies are founded in early spring by one or more queens who mated the previous summer and hibernated throughout the winter. The foundress queen constructs a small nest containing just a few brood cells. After laying a small complement of eggs, she feeds and cares for her offspring until they emerge as adults. These individuals (all females) become her workers. They assume all brood care, foraging, and housekeeping duties. The queen continues to lay eggs and the colony grows larger throughout the summer. In early fall, the colony structure begins to break down. Unfertilized eggs give rise to males who mate with newly emerging females that will overwinter and found new colonies.

Ants

The ant colonies show the most developed social life behaviour, their number varies from dozens to millions. The colony includes polymorphic forms and is developed by the fertilised queen or by the migrants of an initial parent colony. Ants are cousins of honeybees and wasps but while bees and wasps are diurnal and sleep in the night, ants are busy working day and night. Ants have no wings, except in sexual forms in breeding season, and therefore their job of travelling to long distances in search of food is very difficult, but addicted to work as they are and having never-say-die spirit, make them excellent foragers that work round the clock, apparently without any rest. Ants have the highest developed social system, next only to man, with no apparent conflict seen in the society. A colony may have few thousand to over 500,000 individuals. The nests are built in various designs and are called formicaria. Extreme devotion to duty and 'Work is worship' attitude binds them together. Like honey bees, they have polyethism, which means castes are specialized to carry out specialized duties in the colony. For example, the queen has large abdomen to lay a lot of eggs (2-3 million in a year), males fertilize her, workers have broad, sharp mandibles for cutting and chewing and the soldiers have large head that bears sharp dagger-like mandibles for fighting. Female workers and soldiers are sterile. Ants have poor eyesight and are deaf, but they communicate using a very sophisticated chemical language. For communication, they have glands that release pheromones. Trophollaxis, or the exchange of food, glandular secretions, and enzymes among members of a colony, is sustained by constant antennal stroking, licking, and nuzzling during which they trade food, glandular secretions, and enzymes. The majority of ant species dig nests in the ground or in wood, while some make suspended nests on trees composed of soil, cardboard, wax, or silk, and some, such as safari ants, do not build nests at all. Desert ants build crater-like nests or mounds in which they are able to maintain temperature much below the outside heat. The Tropical ant (*Oecophylla*) makes nest by webbing the leaves with silken thread that is produced by their larvae.

Like honeybees, they have polyethism, which means castes are specialized to carry out specialized duties in the colony.

Castes Differentiation among Ants

According to Imms (1948) at least 29 distinct types of morphologically different individuals are known. The ant shows an extreme case of polymorphism. The main castes of ants are queens, workers and mates (Refer Figure 3.12).

Queen: Queens are the fertile females. Queen is largest in size in comparison to other castes of their species. The antennae and legs are relatively shorter and stouter and the mandibles are well developed. Some species are winged 227 while some species are wingless. Usually large individuals are termed macrogynes and dwarf ones, microgynes. Unlike honeybees, a colony of ants contains several queen. An egg laying worker, gynaecoid, occurs in colony. She becomes normal queen if queen is lost due to any reason. Rarely there occur some peculiar individuals called gynandromorphy. They bear external secondary sexual characters of both male and female.

Workers: Sterile female members of ant colony are called workers. These are smallest in size and are characterized by a reduced thorax, and small eye. A worker shows mostly dimorphism, i.e., large and dwarfs. The larger workers are called the macregates and dwarf individuals as micregates. Macregates are called the wrestlers of the colony for their ability to lift too many weights. They also have amazing sense of direction.

Soldiers are modified workers (sterile female). They are without wings, with distinct heads and powerful. They protect the colony from enemies. Besides protection they serve to crush seeds and other hard food material. In an ant colony number of army ants is very huge, it can be up to 22 million individuals. While on march they eat up everything edible in their path. Army ants (Eelton) have three types of workers. Small worker perform the task of feeding the developing broods. Intermediate size of workers works as foragers or scout ants. They search for the food site. Largest size of workers serves as soldiers who defend their colony. Some soldiers attack the colony of the insects and capture the young larvae and pupae of other ant colonies. Their captured larvae and pupae after hatching works as slaves in colony.

Males: These are small, fertile winged individuals. They bear proportionately smaller head, reduced mandibles, longer antennae, well developed reproductive organs and genitalia. The larger individuals' arc called the macraners and the smaller one micraners.

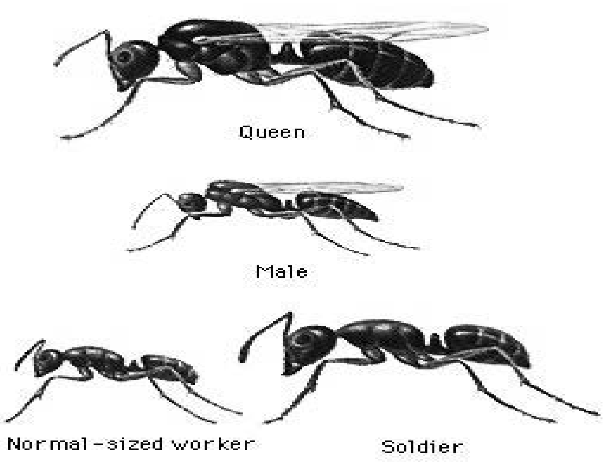


Fig. 3.12 *Cast Differentiation of Ant*

Termites

The termites construct the termitarium with various facilities like controlled temperature and defense against predators and harmful fungi. Termites were the first animals which started living in colonies and developed a well organised social system about 300 million years ago, much earlier than honey bees, ants and human beings. Although termites do not exceed 3-4 mm in size, their queen is a 4 inch long giant that lies in the royal chamber motionless, since its legs are too small to move its enormous body. Hence, workers have to take care of all its daily chores. Termite queen is an egg-laying machine that reproduces at an astonishing rate of two eggs per second. Generally the queen of a termite colony can lay 6,000 to 7,000 eggs per day, and can live for 15 to 20 years. The other castes, workers and soldiers are highly devoted to the colony, working incessantly and tirelessly, demanding nothing in return from the society. Soldiers have long dagger-like mandibles with which they defend their nest and workers chew the wood to feed to the queen and larvae and grow fungus gardens for lean periods. Nasutes are specialized soldiers which specialize in chemical warfare. They produce a jet of highly corrosive chemical from their bodies that can dissolve the skin of enemies and can also help in making galleries through the rocks. The colony lives in the nest which is composed of a queen chamber in the center and many galleries with ventilators. The colonies are found in humid situations under stones, in the wood and on the wall of buildings. The vegetable matter collected by the workers forms the food of the colony. The larvae and queen feed on specific secretion by the workers. The Ambrosia fungus is grown in the fungus gardens in the nest which is used as a food.

Advantages of Social Behaviour in Insects

Following are the advantages of social behaviour in insects:

- Many insects advanced to live in large and cooperative colonies. Their strength also lies in their numbers.
- Social insects work together to find food and other resources for survival and to communicate with each other to help the community.

- They are capable of providing defense to their home and resources when under attack.
- Social insects can also compete with other insects and even larger animals for their territory and food.
- They can quickly construct a shelter and expand it as needed.
- Division of labour in social insects ensures the work to be done quite efficiently.

3.7.2 Symbiosis

Symbiosis is an interspecific relationship in which two different organisms interact with each other for food and shelter. Such type of relationship is necessary for the different organisms to fulfill their needs. It is an association of different insects and other animals for mutual benefit. All the associates are called as **symbionts** and are benefitted. Symbiotic relations among different insects and other animals are established for different interests, such as for food, protection, luxuries of life and even by accident.

The best mutualistic association between flowering plants and insects is pollination. Pollination is a mutualism in which two interactors benefitted from each other, i.e., host plant obtains the service of insect pollination while in return insects get the nectar from the plants. An interesting example is of a certain beetle that lives in the termite nest and gives off some secretion through a glandular knob of the abdomen. The secretion is continuously licked by termites.

To help defend themselves in their environment, many insects form symbiotic connections with other creatures. These are primarily mutualistic partnerships. Aphids and various ant species are an example of this type of connection. The ants get honeydew from the aphids, and the ants carry the aphids inside their nests at night to protect them from predators, and then escort them back to a plant the next morning. This ant species has even been observed gathering aphid eggs and storing them in their nest's storage chambers in order to survive the winter months.

Symbiotic relations between ants and termites with several animals have been reported by several entomologists, for example nesting of many birds in association with wasps, ants and termites giving mutual protection. Ants have been reported to care for and receive food from aphids, membracidae and scale insects.

There are three general types of symbiosis: mutualism, commensalism and parasitism.

Mutualism: Mutualism is a mutually beneficial relationship in which both organisms benefit. Each individual provides an advantage to the other, enabling them to exploit each other and thereby enhance their chances of survival. The best mutualistic association between flowering plants and insects is pollination. Pollination is a mutualism in which two interactors benefitted from each other, i.e., host plant obtains the service of insect pollination while in return insects get the nector from the plants.

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Commensalism: Commensalism is loosely defined as a symbiotic relationship in which one organism benefits and the other is unaffected. A good example of a commensalism is that of smaller organisms 'hitching' a lift on larger organisms (this is known as Phoresy). The smaller organism derives benefit from the other organism and the larger organism is unaffected. The most commonly described phoretic associations are those occurring between different groups of arthropods. Mites may be the ultimate commensals. These tiny arachnids live on the bodies or in the nests of thousands of species (including humans). While some mites are parasitic, most are far too small and passive to have any effect. Several species of commensal mites have evolved specifically to live on humans.

Parasitism: Parasitism is a relationship that is beneficial for one organism and harmful for the other. A tapeworm is a parasite that gains an advantage by hurting another organism, its host. In this case the parasite feeds on digested material in the intestines, taking nutrition away from the host. One example of a parasitic relationship is that of the varroa mite on honey bees. The small mite will attach to a foraging worker bee and catch a ride into the hive. Once there, it will burrow into a cell containing a larva and lay its eggs on it. When the larva pupates the eggs will hatch and the bee will leave the cell, taking the parasites with it. The mites feed on the bee's blood, weakening its immune system and transmitting diseases.

3.7.3 Adaptations

Insects are adapted to their environment in many ways. An adaptation is an adjustment to the environment so that an animal can fit in better and have a better chance of living. Animals with heavy fur coats are adapted for cold environments. Animals that have webbed feet are adapted for living in the water. Here are some adaptations insects can have:

Insects Adaptation to Environment

Insects have the property of camouflage. By camouflage insects can look like same as their environment so that they cannot be seen by predators such as birds and lizards. Some insects look like sticks, thorns and leaves. This type of adaptation helps insect survive by merging with their surroundings so they are not eaten or so that prey does not see them hiding.

Insects can have adapted feet and legs. There are many different types of insect legs, such as running, jumping, swimming and digging. These adaptations help them to survive in the environment that they live in (Grasshoppers have long, strong hind legs that help them jump. This adaptation helps them get away from predators, and jump over tall grasses).Insect antennae can be adapted to their environment. Insects with large eyes do not need extra help seeing and have short antennae. Insects with long antennae probably have very little eyes.

Insect's Adaptation to Mouthparts

Insects can also have adapted mouthparts. There are chewing, sucking, lapping and sponging mouthparts. The most basic type of mouthpart an insect can have are called chewing mouthparts. Chewing mouthparts are generally found in insects that eat plants and sometimes other animals. Cockroaches, beetles, grasshoppers, caterpillars and crickets have chewing mouthparts.

Lapping mouthparts are found in insects that like to consume nectar from plants. They use these mouthparts to drink the sweet nectar from flowers. Lapping mouthparts are made up of the same pieces as chewing mouthparts, but they are assembled differently. Lapping mouthparts are long, flexible straw-like mouthparts that can be inserted deep into flowers. Butterflies have mouthparts that lap. Sucking mouthparts are found on other insects. Sucking mouthparts feature the same parts as chewing mouthparts, but they are modified to sucker plant or blood juices. Insects suck the juices from plants with their mouths. Other insects take blood from animals or other insects with their mouthparts. Mosquitoes have sucking mouthparts. Stink bugs also have sucking mouthparts. House flies have sponging mouthparts to slurp up food.

Insect Adaptations to Habitats

Insects live in many different habitats and there are many different types of legs adapted to survive in their habitat. Insects that live in the water are called aquatic. Aquatic insects have legs adapted for swimming. Some aquatic insects have long legs that are used like oars to help the insect swim. Other insects have very short, fat legs that beat quickly for fast swimming.

Some insects do not swim they walk on top of the water. These insects are very skinny and small and have long, thin legs that keep them on top of the water instead of falling through the water.

Giant water bugs have grasping front legs to catch prey. Their hind legs are long and strong for swimming. Water striders walk on water. Their legs are long and skinny. Their legs help balance out their weight so that they do not break through the water and drown.

Whirligigs have long front legs that help them catch food. Their middle and hind legs are very short and fat, and beat very fast to help them swim quickly.

Insects that need to run very fast usually have long, thin legs. Cockroaches have adapted long and thin legs to help them run away from predators quickly.

Check Your Progress

24. What does the term insect behaviour mean?
25. How is Eusociality characterised?
26. What is a social insect?
27. What is symbiosis.
28. How do ants communicate?

3.8 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Bioluminescence is an amazing natural phenomenon in which an organism produces and emits light due to a chemical reaction where the chemical energy is converted into light energy.
2. Luciferins are a class of light-emitting heterocyclic compounds named after the Latin word lucifer, which means 'light bringer'.
3. Some insect that have bioluminescence are as follows:
   - Coleoptera (Beetles)
   - Glowworm
   - Fire flies
4. Bioluminescence is assumed to have functional relevance in primitive forms of life. For example, in many arthropods, the light from bioluminescence is used to attract the opposite sex for mating, to attract prey, or it may be used for defense.
5. Communication among animals is essen-tial for their well-being. Almost all animals communicate through chemicals produced by glands within the body.
6. Pheromone is a chemical that is produced and released into the environment by an animal which affects the behaviour of another animal of the same species. Pheromones are substances that are created as messengers and influence the behaviour of other insects or animals. They are primarily carried by the wind, although they can also be deposited in soil, vegetation or other objects.
7. Pheromones differ from visual or auditory cues in several ways. They travel slowly, do not dissipate rapidly, and have a vast range of effectiveness. Pheromone detection does not require sound or vision receptors, and pheromone direction is not confined to straight lines.
8. Pheromones were discovered by accident in the 18th century. Bonnet, a French biologist, discovered the ant trail. Bonnet set up an ant colony on one end of a table and a small pile of sugar on the other.
9. Pheromones are chemical in nature. Chemical signals are particularly well-developed in insects and mammals. These chemical signals may be either volatile or non-volatile. Some chemical signals are designed to last only for a short time and hence, are volatile. They tend to have low molecular weights.

Example of such volatile chemical signals are the chemicals used by ants to signal alarm which fades within a minute or even less.

10. Following are the types of pheromones:
    - Aggregation pheromones
    - Alarm pheromones
    - Epideictic pheromones
    - Releaser pheromones
11. Aggregation pheromones are produced by one or the other sex, these pheromones attract individuals of both sexes.
12. Epideictic pheromones are different from territory pheromones, when it comes to insects. It was observed by a scientist named Fabre, that how 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.
13. Neurons are usually divided into three categories, depending on their function within the nervous system
    - Afferent or sensory neurons
    - Efferent or motor neurons
    - Internuncial or association neurons
14. Individual nerve cells connect with one another through special junctions, called synapses.
15. Diapause is a developmental pause that has the effect of facilitating survival in unfavourable conditions, but it is not immediately linked to the unfavourable environment. It is characterised as a physiological state of dormancy or developmental halt in which most life functions are shut down. This is a survival adaptation that is typically seen in arthropods.
16. Diapause can be either obligatory or facultative:
    - Obligatory diapause: In obligatory diapause every individual in every generation enters diapause. Obligatory diapause is most often associated with univoltine insects (means insects having one generation per year).
    - Facultative diapause: In some species of insects, some generations may be completely free of diapause while in other generations some or all of the insects may enter diapause. Insects with facultative diapause undergo a period of suspended development only when conditions require it for survival. Facultative diapause is found in most insects and is associated with bivoltine (having two generations per year) or multivoltine insects (more than two generations per year).
17. Termination, as the name implies, terminates the diapause. By the end of the termination phase, a physiological state is reached, in which direct development may overtly resume. However, certain insects rely on specific environmental stimuli to trigger the termination of diapause.

18. Diapause is caused by a lack of ecdysone, which prevents growth and moulting in larvae and pupae, as well as possibly in late embryonic stages. The absence of the corpus allatum hormone causes the oocytes to fail to mature during adult diapause. The neurosecretory cells of the brain control the action of both the prothoracic gland and the corpora allata, and their failure to function during diapause is due to their inactivity.
19. Mimicry is the superficial but striking likeness in form, colour, attitude, and activity of one creature to another or to inanimate objects. This aids the organism in a variety of ways, including concealment, defense, and other benefits. The word mimicry comes from the Latin word mimicus, which means imitation or simulation.
20. The organism that mimics is known as a mimic, while the organism that copies is known as a model.
21. In concealing mimicry animals develop cryptic colours and blend with surrounding. Spiders resemble in space and colour to the flowers on which they live. These predators are not easily distinguished from the flowers. Whereas, in alluring mimicry type the predator possesses some attraction to appeal its prey. The deceive prey become a victim. Certain spiders mimic the flowers of orchid and insects are attracted to collect honey. Deep sea Angler fish Lophius has first ray of dorsal fin modified to illicium and it works as bait.
22. Mullerian mimicry is a natural phenomenon in which two or more well-defended species, often foul-tasting and that share common predators, have come to mimic each other's honest warning signals, to their mutual benefit.
23. The phenomenon of automimicry refers to how certain members of a species benefit from their likeness to other members of the same species.
24. An insect behaviour refers to the various actions of an insect in response to a stimulus or to its environment. It covers a wide range of activities, such as feeding, locomotion, grooming, reproduction, learning, migration, and communication.
25. Eusociality is an extreme form of social behaviour found in just a few types of animals and is characterised by the following:
    - Occurrence of polymorphic forms each assigned with a different function.
    - Worker members of the colony provide food and care to the reproductive member and the early developmental stages of the colony.
    - Division of labour in the colonies.
    - The presence of several generations in a single hive/nest at the same time.
26. The term social insect generally refers to any of numerous species of insects that live in colonies and exhibit three characteristics namely group integration, division of labour and overlap of generations. In insects social life has evolved only in two orders, namely, Isoptera (termites) and Hymenoptera (bees, wasps and ants) which make a nest and live in colonies of thousands of individuals that practice division of labour and social interaction.

27. Symbiosis is an interspecific relationship in which two different organisms interact with each other for food and shelter. Such type of relationship is necessary for the different organisms to fulfill their needs. It is an association of different insects and other animals for mutual benefit.
28. Ants have poor eyesight and are deaf, but they communicate using a very sophisticated chemical language. For communication, they have glands that release pheromones.

3.9 SUMMARY

- Bioluminescence is an amazing natural phenomenon in which an organism produces and emits light due to a chemical reaction where the chemical energy is converted into light energy.
- The Greeks and Romans were the first to report the characteristics of luminous organisms. Aristotle (384-322 BC) described 180 marine species and was the first to recognize 'cold light'.
- Bioluminescence can be defined as the emission of light by a living creature for the purpose of survival or reproduction.
- Bioluminescence is one of the principal communication systems in deep sea, and it occurs mostly in the marine environment.
- Bioluminescence is caused by a chemoluminescence reaction in which the pigment luciferin is catalysed by the enzyme luciferase.
- Many species produce luciferase, which helps in the speeding up of reactions. Some organisms bind oxygen with luciferin in a photoprotein. It lights up the moment some ion is present.
- Luciferins are a class of light-emitting heterocyclic compounds named after the Latin word lucifer, which means 'light bringer'.
- The beetles have the largest number and variety of luminescent species. They are found mainly in the superfamily Elateroidea, which includes Fireflies (*Lampyridae*), Railroad worms (*Phengodidae*), Click beetles (*Elateridae*), and related families.
- Railroad worms emit the widest range of colors among luminescent beetles, including some of the most spectacular examples with larvae and females having rows of lateral lanterns along the body emitting green-orange light and, in addition South-American species with cephalic lanterns emitting from yellow-green to red light depending on the species.
- In the larval stage, bioluminescence assumes mainly defensive functions but attraction of prey is also seen in the larvae of the Brazilian *Pyrearinuster mitilluminans* Click beetle, which display the phenomenon of luminous termite mounds.
- Fireflies have light-generating structures located in their abdomens wherein light is generated when the chemical luciferin reacts with calcium, oxygen,

ATP and the enzyme responsible for the bioluminescence, luciferase, inside the organ.

- Bioluminescence is assumed to have functional relevance in primitive forms of life. For example, in many arthropods, the light from bioluminescence is used to attract the opposite sex for mating, to attract prey, or it may be used for defense.
- In firefly, light is used as a mating signal.
- In some species, bioluminescence induces members of the same species to congregate, enhancing mating chances indirectly. Because the females of some Lampyridae species are wingless and sedentary, light production is critical for them to attract winged males.
- The most unique example of light acting as a lure for prey is found in the New Zealand glowworm fly, known as *Arachnocampa luminosa*.
- The constant glow of the head area in Railroad worm larvae while walking supports an illumination role, but the circumstances in which the lateral light organs are turned on suggest a defense function.
- Bioluminescence is used to map the distribution patterns of organisms.
- In 2001, scientists in the United States injected Green Fluorescent Protein (GFP) obtained from the jelly fish *Aequorea victoria* (also called as crystal jelly) into the genetic material of the pink bollworm, a cotton pest.
- Communication among animals is essential for their well-being. Almost all animals communicate through chemicals produced by glands within the body.
- Pheromone is a chemical that is produced and released into the environment by an animal which affects the behaviour of another animal of the same species.
- Karlson and Luscher (1959) coined the term pheromone, which is derived from two Greek words: pherein, to carry and harman, to excite. The term was originally assigned to insect sex attractants, but it was later broadened to include a variety of chemicals released into the environment that have varied functions in practically all animals.
- Pheromones are substances that are created as messengers and influence the behaviour of other insects or animals. They are primarily carried by the wind, although they can also be deposited in soil, vegetation or other objects.
- Pheromones differ from visual or auditory cues in several ways. They travel slowly, do not dissipate rapidly, and have a vast range of effectiveness. Pheromone detection does not require sound or vision receptors, and pheromone direction is not confined to straight lines.
- Pheromones are unique to each species. Hormones released by exocrine glands are the most common type.
- Pheromones were discovered by accident in the 18th century. Bonnet, a French biologist, discovered the ant trail. Bonnet set up an ant colony on

one end of a table and a small pile of sugar on the other.

- Pheromones are chemical in nature. Chemical signals are particularly well-developed in insects and mammals. These chemical signals may be either volatile or non-volatile. Some chemical signals are designed to last only for a short time and hence, are volatile. They tend to have low molecular weights.
- Aggregation pheromones are produced by one or the other sex, these pheromones attract individuals of both sexes. Its roles include predator defense, partner selection and mass attack to overcome host resistance.
- Aggregation refers to a collection of people gathered in one place, whether they are of one gender or both. Because they frequently result in the attendance of both sexes at a calling location and an increase in density of conspecifics surrounding the pheromone source, male-produced sex attractants have been dubbed aggregation pheromones.
- Females create the majority of sex pheromones, while males produce only a small percentage of sex attractants.
- Some species release a volatile substance when attacked by a predator that can trigger flight (in aphids) or aggression (in bees) in members of the same species.
- Epideictic pheromones are different from territory pheromones, when it comes to insects. Fabre observed and noted how 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.
- Hundreds of pheromones are known with which one sex (usually the female) of an insect species attracts its mates.
- Signal pheromones that can cause short term changes, such as the neurotransmitter release which activates a response.
- Primer pheromones trigger a change of developmental events.
- Territorial pheromones are laid down in the environment and mark the boundaries of an organism's territory.
- Information pheromones are indicative of an animal's identity or territory.
- In animals, sex pheromones indicate the availability of the female for breeding.
- Male animals may also emit pheromones that convey information about their species and genotype.
- Many insect species release sex pheromones to attract a mate and many lepidopterans can detect a potential mate from as far away as 10 km (6.2 miles).
- Pheromones can be used in gametes to trail the opposite sex's gametes for fertilization.

- Pheromones are also used in the detection of oestrus in sows. Boar pheromones are sprayed into the sty, and those sows which exhibit sexual arousal are known to be currently available for breeding.
- Pheromones are produced by defi-nite glands. These glands vary in their structure and location on the body of animals.
- In honey bee phero-mones are liberated from two glands, i.e., mandibular and Nassanoff's.
- Mandibular glands are located in the head region. It is a sac-like structure and their duct opens at the base of the mandible. They are well-developed in the queen and workers but reduced in drones.
- Nassanoff's gland was discovered in 1882 by a Russian biologist, after whom it was named. It is found below the inter-segmental membrane (arthrodial mem-brane) between the 6th and 7th abdominal segments.
- Nassanoff's gland is made up of a number of large cells which opens to the exterior by small ducts.
- Pheromones are employed by various animals to attract the other sex for mating.
- Female insects usually release pheromones by exposing the concerned glands. Generally, they are released at particular time of the day, depending upon the diurnal or nocturnal nature of the animal. The scent thus released excites the approaching male and serves as a guide for reaching the female.
- Many ant species create smell trails to help them navigate. Pheromones have a function in communication among fire ants. After finding a food source, the worker returns to the nest by leaving a trail.
- Worker honey bees are attracted towards each other by scent from Nassanoff's gland.
- Inhibitory pheromones inhibit the action of other pheromones produced by the same species.
- The nervous system of an insect is a network of specialized cells also called as neurons that act as an internal 'information highway'.
- Electrical impulses, i.e., action potentials are generated by these cells and pass over the cell membrane as depolarization waves.
- The action potential is propagated by filament-like processes (dendrites, axons, or collaterals) in each neuron.
- Signal transmission is always unidirectional, with dendrites or collaterals pointing toward the nerve cell body and axons pointing away from it.
- Individual nerve cells connect with one another through special junctions, called synapses.
- Nerve cells are typically found grouped in bundles.
- A nerve is simply a bundle of dendrites or axons that serve the same part of the body.

- A ganglion is a dense cluster of interconnected neurons that process sensory information or control motor outputs.
- Insects have a very simple Central Nervous System (CNS), with a dorsal brain connected to a ventral nerve cord made up of paired segmental ganglia running along the ventral midline of the thorax and abdomen, similar to most other arthropods.
- A short medial nerve (commissure) connects the ganglia in each segment, while intersegmental connectives connect the ganglia in adjacent body segments.
- The Central Nervous System (CNS) resembles a ladder in appearance, with commissures serving as the rungs and intersegmental connectives serving as the rails.
- In more advanced insect orders there is a tendency for individual ganglia to combine (both laterally and longitudinally) into larger ganglia that serve multiple body segments.
- An insect's brain is a complex of six fused ganglia (three pairs) located dorsally within the head capsule.
- Protocerebrum is the first pair of ganglia are largely associated with vision; they innervate the compound eyes and ocelli.
- Deutocerebrum is a second pair of ganglia process sensory information collected by the antennae.
- The Peripheral Nervous System (PNS) consists of all of the motor neuron axons that radiate to the muscles from the ganglia of the CNS and stomodeal nervous system plus the sensory neurons of the cuticular sensory structures (the sense organs) that receive mechanical, chemical, thermal, or visual stimuli from an insect's environment.
- A stomodaeal (or stomatogastric) nerve system innervates the majority of an insect's internal organs.
- Learning is a cognitive process in which one's behaviour changes as a result of an experience.
- The brain mechanisms used by ants in a path integration orientation system, for example require the computation of a homing vector from hundreds of individual direction and distance (measurements).
- Diapause is a developmental pause that has the effect of facilitating survival in unfavorable conditions, but it is not immediately linked to the unfavorable environment.
- Diapause is characterised as a physiological state of dormancy or developmental halt in which most life functions are shut down. This is a survival adaptation that is typically seen in arthropods.
- In temperate climates, diapause is primarily concerned with surviving through

the cold winter months when normal growth is impossible, however in the tropics, it may help with survival during the dry season, which is marked by a lack of moisture and food.

- Diapause is triggered by unfavourable conditions, such as heat, cold, or harsh environmental conditions and it is a natural response of insects to protect themselves from these conditions.
- Diapause in insects is mainly caused by adverse conditions, such as a lack of food, variations in day length and temperature, and so on.
- During the diapause of insects, concentration of growth hormones starts decreasing and thus slow down the process of development.
- In many animals, the impact of external influences on a critical stage of development affects whether or not diapause will occur. This sensitive period occurs well before the onset of diapause.
- Prodoxus y-inversus is a moth that can sleep for up to 19 years. This is the longest diapause ever documented in biological research. This moth is found in Southwestern Mexico and the United States.
- Diapause can be either obligatory or facultative.
- In obligatory diapause every individual in every generation enters diapause.
- Obligatory diapause is most often associated with univoltine insects, which means insects having one generation per year.
- In some species of insects, some generations may be completely free of diapause while in other generations some or all of the insects may enter diapause.
- Facultative diapause is found in most insects and is associated with bivoltine (having two generations per year) or multivoltine insects (more than two generations per year).
- Induction occurs much before the onset of unfavourable environmental conditions.
- The induction phase is followed by the preparation phase. In this phase, the behavioural and physiological preparations for diapause may take place.
- Initiation is the most important stage of diapause. The initiation stage is characterized by cessation of morphological development, which is commonly followed by regulated metabolic suppression.
- Mobile diapause stages may continue accepting food, building of energy reserves and seeking suitable microhabitat.
- Physiological preparations for the period of adversity may take place and intensity of diapause may increase. These include a change in colour, moulting into a diapause stage or release of special enzymes.
- The neuroendocrine system of insects consists primarily of neurosecretory cells in the brain, such as corpora cardiaca, corpora allata and the prothoracic glands.

- Prothoracicotropic hormone stimulates the prothoracic glands to produce ecdysteroids that are required to promote development.
- Adult diapause is often associated with the absence of Juvenile Hormone (JH), while larval diapause is often associated with its presence.
- Diapause Hormone (DH) regulates embryonic diapause in the eggs of the Silkworm moth, *Bombyx mori*.
- Diapause Hormone (DH) is released from the subesophageal ganglion of the mother and triggers trehalase production by the ovaries.
- Diapause is caused by a lack of ecdysone, which prevents growth and moulting in larvae and pupae, as well as possibly in late embryonic stages.
- The absence of the corpus allatum hormone causes the oocytes to fail to mature during adult diapause.
- The neurosecretory cells of the brain control the action of both the prothoracic gland and the corpora allata, and their failure to function during diapause is due to their inactivity.
- Mimicry is the superficial but striking likeness in form, colour, attitude, and activity of one creature to another or to inanimate objects.
- The organism that mimics is known as a mimic, while the organism that copies is known as a model.
- Protective mimicry includes imitation of organism to other organisms or surrounding in form of colour or behaviour.
- In concealing mimicry animals develop cryptic colours and blend with surrounding.
- In alluring mimicry type the predator possesses some attraction to appeal its prey. The deceive prey become a victim.
- Mullerian mimicry is a natural phenomenon in which two or more well-defended species, often foul-tasting and that share common predators, have come to mimic each other's honest warning signals, to their mutual benefit.
- The phenomenon of automimicry refers to how certain members of a species benefit from their likeness to other members of the same species.
- An insect behaviour refers to the various actions of an insect in response to a stimulus or to its environment.
- Some insect behaviours are driven by the effects of the pheromones. Insects release chemicals that affect the behaviour of the other members of the same species as the latter perceive the released pheromones.
- In general, there are two types of behaviour observed in animals, i.e., innate behaviour and learned behaviour.
- The innate behaviour is one that is inherent or instinctive. It is genetically wired to the organism.

- Learned behaviour is a type of behaviour that the animal acquires through experience or learning.
- The term social insect generally refers to any of numerous species of insects that live in colonies and exhibit three characteristics namely group integration, division of labour and overlap of generations.
- Insects known as wasps belong to family Vespidae, about 75,000 species of wasps are known, most of them parasitic or predators.
- Wasps are characterised by two pairs of membranous wings, three pairs of legs and an ovipositor that may be modified as sting in sterile females.
- Wasps can be solitary or colonial, social insects that live in large colonies with thousands of members and build nests. Wasps build several types of nests depending on the species and region.
- The ant colonies show the most developed social life behaviour, their number varies from dozens to millions.
- Ants have the highest developed social system, next only to man, with no apparent conflict seen in the society.
- Ants have poor eyesight and are deaf, but they communicate using a very sophisticated chemical language.
- The majority of ant species dig nests in the ground or in wood, while some make suspended nests on trees composed of soil, cardboard, wax, or silk, and some, such as safari ants, do not build nests at all.
- Desert ants build crater-like nests or mounds in which they are able to maintain temperature much below the outside heat.
- The termites construct the termitarium with various facilities like controlled temperature and defense against predators and harmful fungi.
- Termites were the first animals which started living in colonies and developed a well organised social system about 300 million years ago, much earlier than honey bees, ants and human beings.
- Symbiosis is an interspecific relationship in which two different organisms interact with each other for food and shelter. Insects are adapted to their environment in many ways.
- An adaptation is an adjustment to the environment so that an animal can fit in better and have a better chance of living.
- Animals with heavy fur coats are adapted for cold environments.
- Animals that have webbed feet are adapted for living in the water.
- Insects have the property of camouflage. By camouflage insects can look like same as their environment so that they cannot be seen by predators such as birds and lizards.
- Insects live in many different habitats and there are many different types of legs adapted to survive in their habitat. Insects that live in the water are called aquatic.

- Aquatic insects have legs adapted for swimming. Some aquatic insects have long legs that are used like oars to help the insect swim. Other insects have very short, fat legs that beat quickly for fast swimming.
- Some insects do not swim they walk on top of the water. These insects are very skinny and small and have long, thin legs that keep them on top of the water instead of falling through the water.
- Whirligigs have long front legs that help them catch food. Their middle and hind legs are very short and fat, and beat very fast to help them swim quickly.
- Insects that need to run very fast usually have long, thin legs. Cockroaches have adapted long and thin legs to help them run away from predators quickly.

3.10 KEY TERMS

- **Bioluminescence:** Bioluminescence can be defined as the emission of light by a living creature for the purpose of survival or reproduction.
- **Pheromone:** Pheromone is a chemical that is produced and released into the environment by an animal which affects the behaviour of another animal of the same species.
- **Synapses:** Individual nerve cells connect with one another through special junctions, called synapses.
- **Nerve:** A nerve is simply a bundle of dendrites or axons that serve the same part of the body.
- **Ganglion:** A ganglion is a dense cluster of interconnected neurons that process sensory information or control motor outputs.
- **Protocerebrum:** Protocerebrum is the first pair of ganglia are largely associated with vision; they innervate the compound eyes and ocelli.
- **Deutocerebrum:** Deutocerebrum is a second pair of ganglia process sensory information collected by the antennae.
- **Obligatory diapause**: In obligatory diapause every individual in every generation enters diapause.
- **Photoperiod:** A photoperiod is the alternating phases of light and dark in the day.
- **Mimic**: The organism that mimics is known as a mimic.
- **Model**: The organism that copies is known as a model.
- **Automimicry:** The phenomenon of automimicry refers to how certain members of a species benefit from their likeness to other members of the same species.
- **Insect behaviour:** An insect behaviour refers to the various actions of an insect in response to a stimulus or to its environment.
- **Innate behaviour:** The innate behaviour is one that is inherent or instinctive. It is genetically wired to the organism.

- **Learned behaviour:** Learned behaviour is a type of behaviour that the animal acquires through experience or learning.
- **Social Insect:** The term social insect generally refers to any of numerous species of insects that live in colonies and exhibit three characteristics namely group integration, division of labour and overlap of generations.
- **Symbiosis**: Symbiosis is an interspecific relationship in which two different organisms interact with each other for food and shelter.

3.11 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. What is bioluminescence and how it originated?
2. Draw the structure of luciferin.
3. Write a brief note on insects that have bioluminescence.
4. Why is bioluminescence significant in insects?
5. What is the chemical nature of pheromones?
6. Distinguish between information, releaser and signal pheromone.
7. Briefly explain the functions of pheromones.
8. What is nervous integration of insects?
9. Write about the different organisms that possess diapause.
10. What are the different stages of diapause?
11. Write briefly about the factors that regulate diapause.
12. What is mimicry? Write about the types of mimicry in insects.
13. Briefly discuss about insect behaviour and its types.
14. Write a short note on social life of insects.

Long-Answer Questions

1. Discuss in detail about bioluminescence and its significance in insects.
2. Elaborate a note on different light producing organs in insects.
3. Explain the mechanism of bioluminescence in insects.
4. Give a detail account on pheromones, their types, chemical nature and functions.
5. Describe nervous integration, learning and memory.
6. Draw a well labelled diagram to show different types of neuron.
7. Elaborate a note on diapause in insects.
8. Give a detailed description of mimicry in insects.
9. Explain how insect behave.
10. Describe the Social life of insects.
11. Discuss in detail about symbiosis and adaptations in insects.

3.12 FURTHER READINGS

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UNIT 4 REPRODUCTION, FERTILIZATION, DEVELOPMENT AND METAMORPHOSIS

Structure

4.0 INTRODUCTION

Insect reproductive system comprises of paired sexual gonads, the ovaries of the female and testes of the male. Transfer of sperm from a male to a female reproductive tract performs numerous activities. It involves finding location of one sex by counterpart, courtship, pairing, copulation and eventually, insemination of female. Generally insects are oviparous that is they lay eggs. Some insects produce larvae or nymphs rather than laying eggs and thus this phenomenon called as viviparity. Some insects reproduce by means of parthenogenesis. In a few other insects, reproduction mode is associated with polyembryony or paedogenesis. Most insects reproduce oviparously, i.e., by laying eggs. The eggs are produced by the female in a pair of ovaries. Sperm, produced by the male in one testis or more commonly two, is transmitted to the female during mating by means of external genitalia. The sperm is stored within the female in one or more spermathecae. At the time of fertilization, the eggs travel along oviducts to be fertilized by the sperm and are then expelled from the body, in most cases via an ovipositor.

Female insects are able to make eggs, receive and store sperm, manipulate sperm from different males and lay eggs. Their reproductive systems are made up of a pair of ovaries, accessory glands, one or more spermathecae, and ducts connecting these parts. The ovaries make eggs and accessory glands produce the substances to help package and lay the eggs. Spermathecae store sperm for varying periods of time and, along with portions of the oviducts, can control sperm use. The ducts and spermathecae are lined with a cuticle. The ovaries are made up of a number of egg tubes called ovarioles, which vary in size and number by species. The number of eggs that the insect is able to make varies according to the number of ovarioles, with the rate at which eggs develop being also influenced by ovariole design. In meroistic ovaries, the eggs-to-be divide repeatedly and most of the daughter cells become helper cells for a single oocyte in the cluster. In panoistic ovaries, each egg-to-be produced by stem germ cells develops into an oocyte, there are no helper cells from the germ line. Production of eggs by panoistic ovaries tends to be slower than that by meroistic ovaries. Accessory glands or glandular parts of the oviducts produce a variety of substances for sperm maintenance, transport, and fertilization, as well as for protection of eggs. They can produce glue and protective substances for coating eggs or tough coverings for a batch of eggs called oothecae. Spermathecae are tubes or sacs in which sperm can be stored between the time of mating and the time an egg is fertilized. Paternity testing of insects has revealed that some, and probably many, female insects use the spermatheca and various ducts to control or bias sperm used in favour of some males over others.

The main component of the male reproductive system is the testis, suspended in the body cavity by tracheae and the fat body. The more primitive apterygote insects have a single testis, and in some lepidopterans the two maturing testes are secondarily fused into one structure during the later stages of larval development, although the ducts leading from them remain separate. However, most male insects have a pair of testes, inside of which are sperm tubes or follicles that are enclosed within a membranous sac. The follicles connect to the vas efferens by the vas deferens, and the two tubular vasa deferentia connect to a median ejaculatory duct that leads to the outside. A portion of the vas deferens is often enlarged to form the seminal vesicle, which stores the sperm before they are discharged into the female. The seminal vesicles have glandular linings that secrete nutrients for nourishment and maintenance of the sperm. The ejaculatory duct is derived from an invagination of the epidermal cells during development and, as a result, has a cuticular lining. The terminal portion of the ejaculatory duct may be sclerotized to form the intromittent organ, the aedeagus. The remainder of the male reproductive system is derived from embryonic mesoderm, except for the germ cells, or spermatogonia, which descend from the primordial pole cells very early during embryogenesis.

Often in populations of insects, males of the species emerge first as adults, and thus are available for mating when the females emerge. The usual example of this strategy is in the genus Opifex, a mosquito group in New Zealand, where males immediately mate with the female as she emerges from her pupal shell. Finding and recognizing mates is usually achieved by chemical attractants in the air (called pheromones), appearing at the same food, sometimes by sound, and uncommonly by light flashes or flashing of colours. Sex-attractant pheromones are produced by female moths and perceived in the air by the antennae of males of the species. Many kinds of insects, including flies, beetles, wasps, bees, and butterflies are known to congregate at locations termed leks, where there is no food, water or beneficial resource other than individuals of the same species. These leks are simply a place to locate mates. As might be expected, the different ways in which insect sexes locate and recognize each other are extremely numerous because there are so many insect species.

Fertilization of ova takes place when it moves into the genital organ and some of sperm are liberated from spermatheca. Most of the insect species are diploid (2n) means constituting one set of chromosomes from each parent. Various types of stimuli are involved in the activation of insect ova, such as entrance of sperm cell into the egg via a facilitating structure called the micropyle. Development in fertilized egg called as postembryonic development. Growth phases beginning from egg, through number of immature development stages, such as larvae or nymph to eclosion of adult vary species to species. Developmental changes in form of insects during ontogeny (from egg to adult formation) influence both internal and external structures. These developmental changes are known as metamorphosis of insects. Internal fertilization by insertion of the male intromittent organ into the female genital tract for deposition of sperm is the usual method of copulation. There are exceptions, of course, and the most dramatic is perhaps the bedbug, where males actually pierce the body cavity of the female with their penis to deposit sperm. Springtails (Order Collembola) are exceptional also in that the male produces spermatophores and places them in a circle around the female. The male then performs a courtship dance, encouraging the female to cross the circle. The female then grasps one droplet with her genital opening, which leads to fertilization.

Vitellogenesis also known as yolk deposition is the process of yolk formation via nutrients being deposited in the oocyte, or female germ cell involved in reproduction of lecithotrophic organisms. In insects, it starts when the fat body stimulates the release of Juvenile Hormones (JH) and produces vitellogenin protein. It occurs in all animal groups other than the mammals. In cockroaches, for example, vitellogenesis can be stimulated by injection of juvenile hormone into immature females and mature males. Chemically yolk is lipoprotein composed of proteins, phospholipids and neutral fats along with a small amount of glycogen. The yolk is synthesized in the liver of the female parent in soluble form. Through circulation it is transported to the follicle cells that surround the maturing ovum, and is deposited in the form of yolk platelets and granules in the ooplasm. The mitochondria and Golgi complex are said to bring about the conversion of the soluble form of yolk into insoluble granules or platelets. In mosquitoes infected with *Plasmodium*, vitellogenesis may be manipulated by the parasites to reduce fecundity. In mammalian vitellogenesis, vitellogenin is the major protein, produced by the Vit gene and regulated by oestrogen. The yolk consists of lipids (triglycerides, cholesterol, etc.) and proteins, mainly vitellogenin.

Parthenogenesis, a reproductive strategy that involves development of a female gamete without fertilization. It occurs commonly among lower plants and invertebrate animals (particularly rotifers, aphids, ants, wasps, and bees) and rarely among higher vertebrates. An egg produced parthenogenetically may be either haploid, i.e., with one set of dissimilar chromosomes or diploid, i.e., with a paired set of chromosomes. Parthenogenic species may be obligate, i.e., incapable of sexual reproduction or facultative, i.e., capable of switching between parthenogenesis and sexual reproduction depending upon environmental conditions. Parthenogenesis is sometimes considered to be an asexual form of reproduction; however, it may be more accurately described as an 'incomplete form of sexual reproduction', since offspring of parthenogenic species develop from gametes. Gametes are reproductive cells that result from meiosis (or reduction division)—in which a specialized cell with a (diploid) double set of chromosomes undergoes two fissions of its nucleus. Meiosis gives rise to four gametes, or sex cells, which are haploid—in that each possesses half the number of chromosomes of the original cell.

Fertilization is the fusion of gametes to give rise to a new individual organism or offspring and initiate its development. External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization can then take place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The release of the reproductive material may be triggered by water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans, for example crabs and shrimp, mollusks, for example oysters, squid, and echinoderms, for example sea urchins and sea cucumbers. Pairs of fish that are not broadcast spawners may exhibit courtship behaviour. This allows the female to select a particular male. The trigger for egg and sperm release (spawning) causes the egg and sperm to be placed in a small area, enhancing the possibility of fertilization.

External fertilization in an aquatic environment protects the eggs from drying out. Broadcast spawning can result in a greater mixture of the genes within a group, leading to higher genetic diversity and a greater chance of species survival in a hostile environment. For sessile aquatic organisms, such as sponges, broadcast spawning is the only mechanism for fertilization and colonization of new environments. The presence of the fertilized eggs and developing young in the water provides opportunities for predation, resulting in a loss of offspring. Therefore, millions of eggs must be produced by individuals. The offspring produced through this method must mature rapidly. The survival rate of eggs produced through broadcast spawning is low. Internal fertilization occurs most often in land-based animals, although some aquatic animals also use this method. There are three ways that offspring are produced following internal fertilization: oviparity, ovoviparity and viviparity. In oviparity, fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg. This occurs in most bony fish, many reptiles, some cartilaginous fish, most amphibians, two mammals, and all birds. Reptiles and insects produce leathery eggs, while birds and turtles produce eggs with high concentrations of calcium carbonate in the shell, making them hard. These animals are classified as oviparous. In ovoviparity, fertilized eggs are retained in the female, but the embryo obtains its nourishment from the egg's yolk; the young are fully developed when they are hatched. This occurs in some bony fish, such as the guppy, *Lebistes reticulatus*, some sharks, some lizards, some snakes, such as the garter snake, *Thamnophis sirtalis*, some vipers, and some invertebrate animals, such as the Madagascar hissing cockroach, *Gromphadorhina portentosa*.

A larva (plural larvae) is the juvenile form of an insect. The larva often has a different appearance to the adult and may possess bodily organs that the adult insect does not possess (and vice versa). Larvae need to undergo metamorphosis to reach the adult stage. This separation of larva and adult often means that adult and young do not compete for food. For example, the caterpillar of a butterfly may have a very specific food plant on which it feeds and the adult drinks nectar from flowers. Different types of insect have other names for their larvae, for example, caterpillars are the larvae of butterflies and moths. For insects that undergo incomplete metamorphosis the larvae are also called nymphs. Larvae are frequently adapted to different environments than adults. For example, some larvae, such as tadpoles live almost exclusively in aquatic environments, but can live outside water as adult frogs. By living in a distinct environment, larvae may be given shelter from predators and reduce competition for resources with the adult population. Animals in the larval stage consume food to fuel their transition into the adult form. In some organisms like polychaetes and barnacles, adults are immobile but their larvae are mobile, and use their mobile larval form to distribute themselves. Some larvae are dependent on adults to feed them. In many eusocial Hymenoptera species, the larvae are fed by female workers. In *Ropalidia marginata* (a paper wasp) the males are also capable of feeding larvae but they are much less efficient, spending more time and getting less food to the larvae.

A pupa is the life stage of some insects undergoing transformation between immature and mature stages. Insects that go through a pupal stage are holometabolous: they go through four distinct stages in their life cycle, the stages thereof being egg, larva, pupa, and imago. The processes of entering and completing the pupal stage are controlled by the insect's hormones, especially Juvenile Hormone (JH), prothoracicotropic hormone, and ecdysone. The act of becoming a pupa is called pupation, and the act of emerging from the pupal case is called eclosion or emergence. The pupae of different groups of insects have different names, such as chrysalis for the pupae of butterflies and tumbler for those of the mosquito family. Pupae may further be enclosed in other structures, such as cocoons, nests, or shells.

Metamorphosis is a biological process by which an animal physically develops after birth or hatching, involving a conspicuous and relatively abrupt change in the animal's body structure through cell growth and differentiation. Some insects, fish, amphibians, mollusks, crustaceans, cnidarians, echinoderms, and tunicates undergo metamorphosis, which is often accompanied by a change of nutrition source or behaviour. Animals can be divided into species that undergo complete metamorphosis (holometaboly), incomplete metamorphosis (hemimetaboly), or no metamorphosis (ametaboly). Scientific usage of the term is technically precise, and it is not applied to general aspects of cell growth, including rapid growth spurts. References to 'metamorphosis' in mammals are imprecise and only colloquial, but historically idealist ideas of transformation and morphology, as in Goethe's Metamorphosis of plants, have influenced the development of ideas of evolution. In simple metamorphosis the immature insects and the adults are similar in appearance, and differ mostly in size. In complete metamorphosis immature insects and the adults have different forms, often live in different habitats, and may have very different behaviour.

In this unit, you will study about male and female reproductive organs in insect and their modifications, physiology of reproduction, mating, transfer of sperm, vitellogenesis, sperm storage, polyembryony and parthenogenesis, fertilization and embryonic development, events before, during and after fertilization, various types of larva, pupa and their significance, metamorphosis in insect, types of metamorphosis, theories of metamorphosis and importance of metamorphosis.

4.1 OBJECTIVES

After going through this unit, you will be able to:

- Discuss about male and female reproductive organs in insects
- Elaborate anatomy and physiology of insect reproductive systems
- Understand the means of sperm transfer by male
- Explain about the process of vitellogenesis
- Describe about fertilization and embryonic development
- Discuss the how does sperm stored and used for fertilization
- Explain the various types of larva, pupa and their significance
- Describe metamorphosis in insect

4.2 REPRODUCTIVE ORGANS IN INSECT

Reproduction in most of the insect species is bisexual. Egg cell produced by female insect develops when fuse with the spermatozoa cell introduced by the male. Insect reproductive system comprises of paired sexual gonads that is the ovaries of female and testes of male (Refer Figure 4.1).

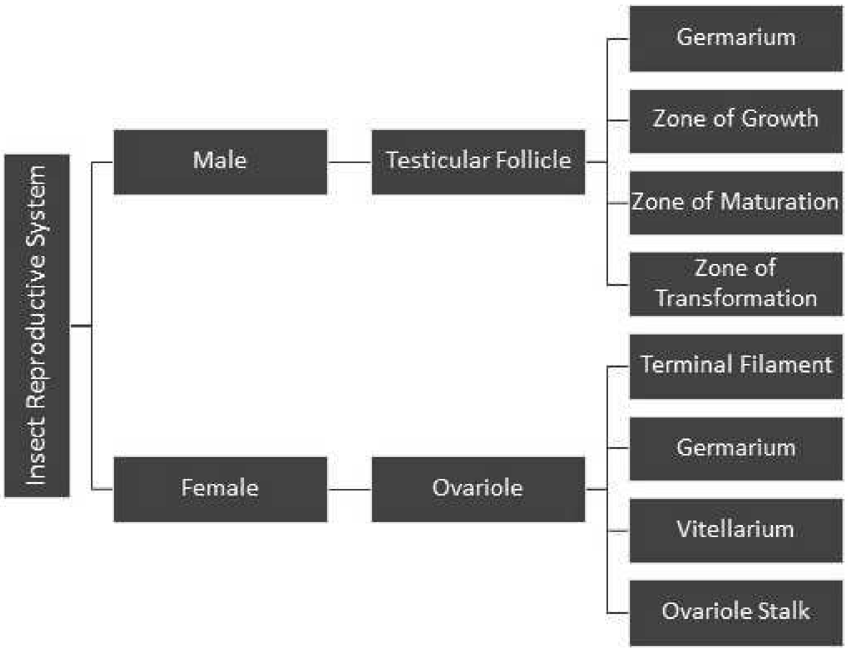

Fig. 4.1 *Major Components of Insect Reproductive System*

4.2.1 Male Reproductive Organs and Their Modifications

Male reproductive system consists of internal reproductive organs, spermatozoa and external reproductive organs. They are explained below:

I. Internal Reproductive Organs

Male reproductive organs have paired testes (in butterfly these fuse to form a single median organ), paired vasa deferens and seminal vesicles, a median ejaculatory duct and various accessory glands (Refer Figure 4.2).

1. Testis

Testes usually lie either above or below gut in abdomen and are near to middle axis. Each testis has a series of testis tubes or testicular follicles. These vary in number and arrangement in different insects. Follicles can open into vas deferens.

Modifications:

- Number of testis tubes ranges from one in ground and aquatic beetles to more than 100 in grasshoppers.
- In some Butterflies, the testicular follicles are not completely separated from each other.
- Testes of flies contain a simple and undivided sac that form single follicle.
- In some insects the follicles are assembled together into many separate lobes. For example, Huhu beetles have each testis comprises of 12-15 lobes and each lobe has 15 follicles.

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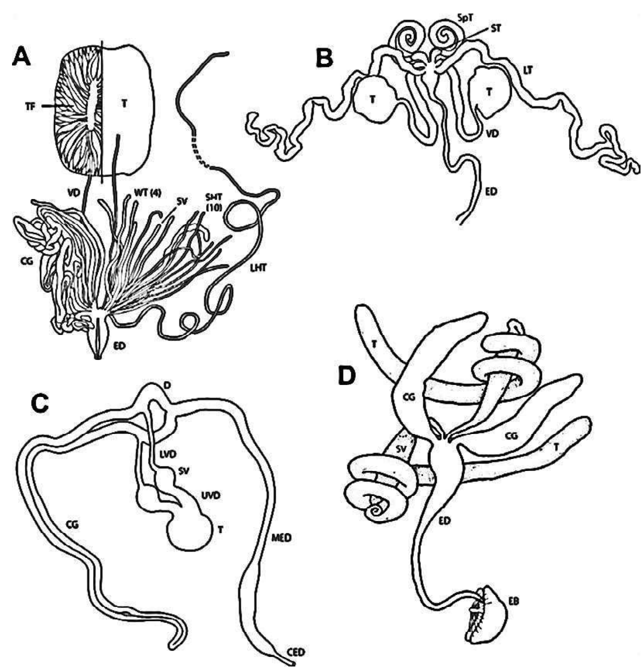

Fig.4.2 *Examples of Male Reproductive Systems*

In above Figure 4.2 examples of male reproductive systems is shown, in which A. shows grasshopper, B. shows blister beetle, C. shows flour moth; and D. shows fruit fly.

The abbreviations used in the above Figure 4.2 are as follows; SV: Seminal Vesicle, D: Duplex, CED: Cuticular Ejaculatory Duct, ED: Ejaculatory Duct, LVD: Lower Vas Deferens, MED: Mesodermal Ejaculatory Duct, T: Testis, TF: Testis Follicle, UVD: Upper Vas Deferens, VD: Vas Deferens and CG: Collateral Gland.

Structure of Testicular Follicle

The wall of testicular follicle has thin epithelium that externally rest on basal lamina. Follicles are joined together by a peritoneal sheath of connective tissue. Each testicular follicle has a series of zones of development. In these zones, male sex cells occur in different phases of development (Refer Figure 4.3). Details of these zones are given below:

- **Germarium:** Distal zone is the germarium in which spermatogonia are produced from germ cells. A prominent apical cell is also present in grasshoppers, cockroaches, bugs and butterflies. Function of apical cell is to supply nutrients to spermatogonia.
- **Zone of Growth:** Each spermatogonium moves proximally into zone of growth. It becomes enclosed within a layer of somatic cells and thus forms a cyst. At first the cysts are rounded, but as they increase in size they become polyhedral. Within the cyst, cell divides mitotically to form a varied number of spermatocytes. Usually each cyst contains 64-256 spermatocytes.
- **Zone of Maturation:** In this zone, spermatocytes undergo meiosis and divide first into two pre-spermatids and then into four spermatids. Thus, spermatocytes undergo two maturation divisions, so that from each

spermatocyte four haploid spermatids are formed.

- **Zone of Transformation:** The most proximal part of follicle has zone of transformation. In this zone, the compressed and rounded spermatids, still enclosed in their cysts, become transformed into flagellated spermatozoa. This process is known as spermiogenesis. At this time the cyst wall normally has ruptured. But the sperm within a bundle remain held together by a gelatinous cap that covers their anterior end. This cap can be removed when sperm enter vas deferens or persist until sperm have been transferred to female.

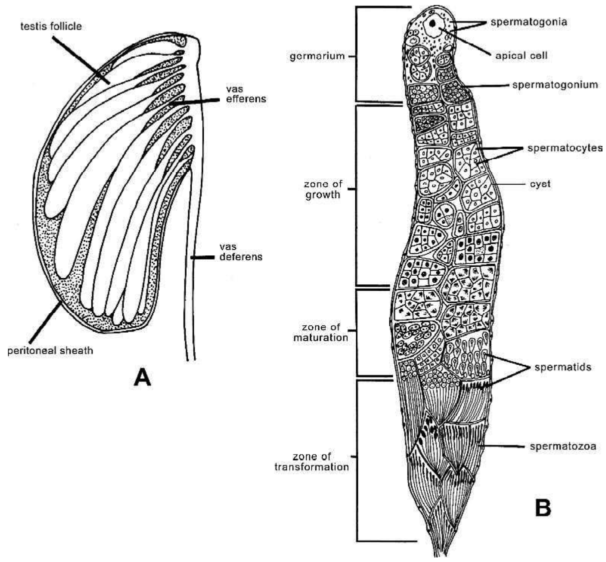

Fig. 4.3 *A. Section through Testis Showing Arrangement of Follicles; and B. Zones of Development in Testis Follicle of Butterfly*

2. Vas Deferens

A thin and short vas efferens (Refer Figure 4.3A) from each follicle arises and joined with the vas deferens (plural: vasa deferentia). Vas deferens is a tube with a thick epithelium, a basement membrane and has a sheet of circular muscle externally. Vasa deferentia placed backside to join into the distal end of ejaculatory duct. A few cells of vas deferens are glandular in nature and secreting their products into the lumen.

3. Seminal Vesicle

In many insects, seminal vesicles are dilations of vasa deferentia. In some insects, such as wasps and mosquitoes, seminal vesicles are present as dilations of ejaculatory duct. Seminal vesicles store sperm before transfer to female reproductive tract.

Modifications:

- Butterflies and moths contain sperm that are briefly stored in expanded area of vasa deferentia. Later sperm are transferred to region of dilations in upper part of ejaculatory duct called as duplex.
- Cellular coating of seminal vesicles is glandular in nature and in fruit flies, it secretes male reproductive proteins.

4. Ejaculatory Duct

The vasa deferentia connect to a central duct known as the ejaculatory duct. It generally opens posteriorly in membrane between ninth and tenth segments of abdomen called gonopore. The epithelium of the ejaculatory duct is one cell thick. As it is epidermal in origin, it is lined with cuticle. Often at least a part of the wall is muscular. Parts of the wall of the duct may be glandular, contributing reproductive proteins to the ejaculate.

Modifications:

- Mayflies have no ejaculatory duct; instead vasa deferentia connect directly to paired genital openings.
- Earwigs have paired ejaculatory ducts whereas, one of the ducts becomes vestigial in some insect, such as European earwig.
- Ejaculatory duct in honeybee is entirely without muscles.
- In some insects, such as Locust, an intricate spermatophore is produced, therefore ejaculatory duct become complex. Thus, ejaculatory duct contains upper and lower ducts connected through a constriction that is a funnel-like structure.
- In Butterflies and moths, the ejaculatory duct is expanded inwardly by unpaired duct that does not have cuticular lining. Thus, this region is known as simplex. Simplex produces spermatophore as these insects have only single pair of accessory glands.

5. Accessory Glands

Accessory glands in male are ectodermal or mesodermal in nature, hence are called as ectadenia or mesadenia, respectively. Different insects show variation in number and arrangement of accessory glands. Accessory glands become functional in adult insect. The glands have role in manufacture of liquid seminal fluid that sustains and nourishes mature sperm while they are in male's genital system. Their secretions are involved in producing spermatophore. Accessory glands are also called as collateral gland.

Modifications:

- Many Beetles, mosquitoes and few sucking insects have ectadenia that leads to ejaculatory duct. Grasshopper and locusts have mesadenia that connects to vasa deferentia or distal end of ejaculatory duct. Some true bugs and beetles have both ectadenia and mesadenia.
- Butterflies have single pair and darkling beetles have two pairs of glands. Locusts have 15 pairs of accessory glands and field cricket has over 600.

II. External Organ of Male Reproductive System

External parts of male reproductive system are collectively called as genitalia. Genitalia involved in coupling with the genitalia of female and introducing sperm into female body. Followings are the basic features of male genitalia (Refer Figure 4.4):

- **Phallic Lobes:** Pair of primary phallic lobes is positioned in posterior ventral surface on ninth segment.
- **Phallomeres:** Phallic lobes split to produce an internal pair of mesomeres and external parameres. Mesomeres and parameres are collectively called as phallomeres.
- **Aedeagus**: Mesomeres joined to produce intromittent organ called as aedeagus. Aedeagus is specialized organ to deliver sperm during copulation. Innermost lining of aedeagus leads to ejaculatory duct known as endophallus. Phallotreme is the opening of duct at tip of aedeagus.
- **Gonopore:** Gonopore is positioned at outside of ejaculatory duct where it leads endophallus. Thus it is internal. Endophallic duct is eversible in many insects and thus gonopore becomes a terminal position at the time of copulation.

Note:

- Parameres develop into claspers, which are very variable in form. They can be attached with aedeagus on a common base called as phallobase.
- Phallus is sometimes used as collective term for parameres and aedeagus. But phallus is also used to mean aedeagus alone. The term penis is sometimes used instead of phallus.

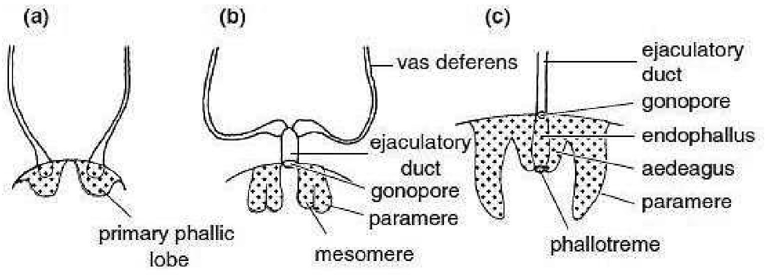

Fig. 4.4 *Diagrams Showing Development and Basic Features of Male Genitalia*

III. Spermatozoa: Male Sex Cell

A. Structure of Sperm

Mature spermatozoa in most insects are flagellate containing head and tail parts. The insect sperm exhibit high variation in morphology. For example, Conehead insects have simple aflagellate disc-like forms of sperm, while fruit flies have giant flagellate sperm that is about 60 mm in length. Flagellate spermatozoa have a characteristic cell membrane that is about 10 nm thick. Cell membrane is covered on exterior by coating of glycoprotein called as glycocalyx.

Larger area of head part is filled by nucleus. DNA material is arranged in strands parallel lying through long axis of sperm. Acrosome is situated in front of nucleus. Acrosome is lined with membrane and is made up of glycoprotein. Axial filament (or axoneme) arises immediately behind nucleus. In many insects, axial filament contains two central tubules with a ring of nine doublets and nine accessory tubules on exterior (Refer Figure 4.5).

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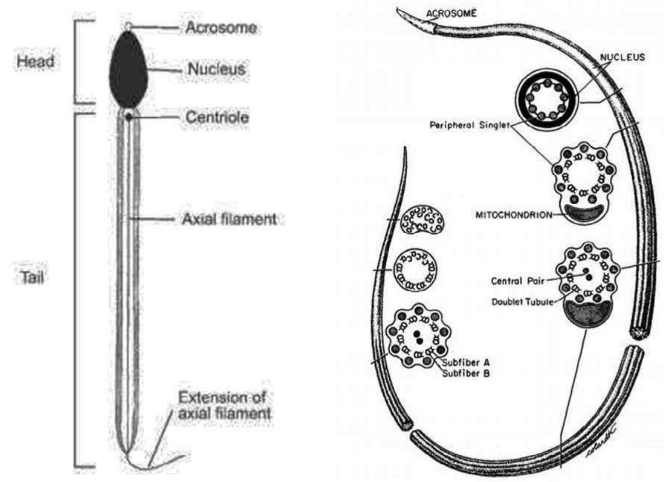

Fig. 4.5 *A. Structure of Sperm; and B. Arrangement of Tubules in Sperm of Caddis Fly*

B. Formation of Sperm: Spermatogenesis

Process of conversion from primitive germ cell spermatogonium into mature germ cell spermatozoa is called as **spermatogenesis**. Zone of germarium in each testicular follicle have germ cells that undergo division and produce spermatogonia. As discussed earlier (in section structure of follicles) three zones of development are present below the germarium comes under process of spermatogenesis. Spermatogenesis (Refer Figure 4.6) takes place in following steps:

- **Growth Phase:** Spermatogonia are the cells that mitotically divide to give rise spermatocytes. It occurs in zone of growth testicular follicle.
- **Maturation Phase:** Eventually spermatocytes meiotically divide to give rise spermatids. Spermatocyte undergoes two number of meiosis. In first meiosis it gives rise pre-spermatids and second meiosis results in formation of spermatids. It occurs in zone of maturation of testicular follicle.
- **Transformation Phase:** Spermatids are transformed into mature sperm (spermatozoa) by process called as spermiogenesis. It occurs in zone of transformation of each testicular follicle. The spermatid formed in meiosis is basically a round cell having usual cell organelles. Spermiogenesis involves a complete reorganization of the sperm cell. Following are details of reorganization of cell organelles in mature spermatozoa during spermiogenesis:
  - o **Acrosome:** In later spermatid, pro-acrosomal granule produced in the cup of the acroblast and rises in size. As spermatid cell grows, the pro-acrosomal granule becomes the acrosome which is cone-shaped and producing a cavity in which an inner cone is derived.
  - o **Nucleus:** As the sperm matures, the nucleus eventually is very long and narrow in appearance. In addition the chromosome fibrils aligned more or less parallel with long axis of nucleus.
  - o **Mitochondria:** The mitochondria joined to constitute a single large body called the nebenkern in the spermatid. It consists of an outside restrictive

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membrane and a central pool of mitochondrial components.

- **Centriole and Axial Filament:** Early spermatids have two centrioles align at right angles to each other and each comprises of nine triplets of tubules in most of the cells. The tubules of the axial filament raises out from the centriole and lastly extend the length of the tail part of mature sperm.

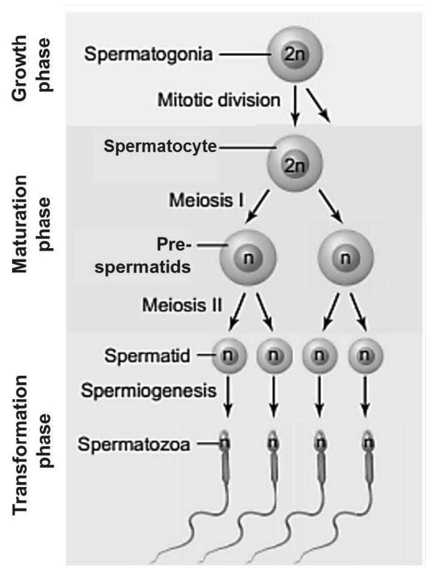

Fig. 4.6 Steps for Spermatogenesis in Male Insects

4.2.2 Female Reproductive Organs and Their Modifications

Like male, female reproductive system consists of internal reproductive organs, ova and external reproductive organs.

I. Internal Reproductive Organs

Female reproductive system contains a pair of ovaries that are joined with a pair of lateral oviducts. These are fuse to lead as a median oviduct that opens posteriorly into a genital cavity. Spermatheca for storing sperm situated at the opening from the genital cavity. In addition, a pair of accessory glands is also present (Refer Figure 4.7).

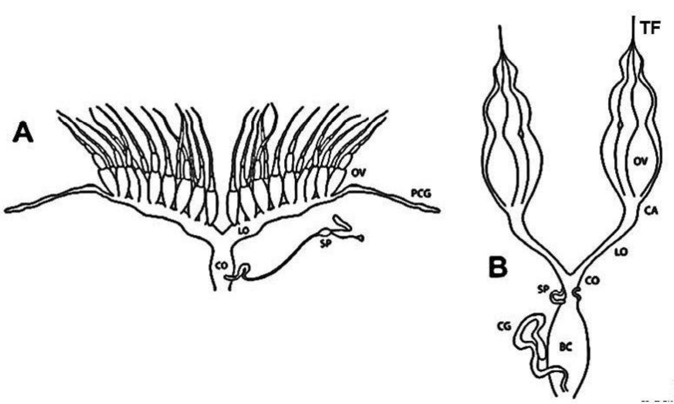

Fig. 4.7 *Female Reproductive System in A. Grasshopper; and B. Bug*

Following are the abbreviations used in above Figure 4.7: TF: Terminal Filaments, CA: Calyx, BC: Bursa Copulatrix, CG: Collateral (Accessory) Glands, CO: Common Oviduct, LO: Lateral Oviduct, OV: Ovariole, PCG: Pseudocolleterial Glands and SP: Spermatheca.

1. Ovary

Paired ovaries situated above or lateral to the gut in abdomen. Each ovary has many egg-tubes called **ovarioles** similar with testicular follicles of testis in male. The oocytes grow and mature in ovarioles. An ovariole is formed distally into a long terminal filament having cellular core lined by tunica propria. Typically each filament from each ovary pooled to produce a suspensory ligament. Ligaments of both sides unite into a center ligament. Butterflies and flies have ovarioles open together into an expansion of oviduct called as calyx. In a few insects, the ligament in ovary is absent and the filaments end free in body cavity.

Modifications:

Number of ovarioles in an ovary varies according to body size, life histories and taxonomic position of insect species. Basically, larger size of species has more number of ovarioles than small size insect. For example:

- Small grasshoppers contain just four ovarioles on each side.
- Fruit flies contains 10–30 ovarioles in its each ovary, while bottle flies have 100 ovarioles.
- Butterflies and moths have four ovarioles in each ovary regardless of their body size.
- Viviparous insects have very reduced numbers of ovarioles. The viviparous insects, such as biting flies, louse flies and tsetse flies contain just two in each ovary.

A. Structure of Ovariole

A typical ovariole is an extended tube that contains the developing eggs arranged in a single chain. Wall of an ovariole is a delicate transparent membrane made up of two layers. An inner coat is a layer of epithelium called as **tunica propria** whose cells rest upon a basement membrane. An outer layer called **tunica externa** is a peritoneal sheath of connective tissue. External sheath has non-penetrating tracheoles. Oxygen used by developing oocytes diffuses in from these tracheoles. Following four zones of developing oocytes are present in an ovariole (Refer Figure 4.8):

- **Terminal Filament**: Terminal filament zone is cylindrical thread-like apical elongation of peritoneal sheath. Filaments of ovarioles of both ovaries unite to produce a common thread called as central ligament. This helps in retaining ovaries in position. It is attached either to fat body of body-wall or to pericardial diaphragm in abdomen.
- **Germarium:** Germarium zone occupies apex of ovariole that is below terminal filament. It has mass of cells through which primordial germ cells are differentiated to form oogonia. Oogonia give rise to oocytes and in some types of ovarioles, also to nutritive cells.

- **Vitellarium:** Vitellarium zone forms maximum part of an ovariole. This has developing oocytes and also nutritive cells. Oocytes in most insects arranged in a linear sequence along ovariole. Each oocyte enclosed in a one-cell-thick layer of follicular epithelium. Follicle cells produce chorion of ova and perform to nourish oocytes. As its name suggests, vitellarium is region in which an oocyte accumulates yolk through a process called as vitellogenesis.
- **Ovariole Stalk:** Ovariole stalk is a thin walled tube opening to oviduct and also called pedicel. When oocyte is maturing it get separated from lumen of ovariole stalk through a solid plug of epithelium. This plug is then degenerate during process of ovulation.

B. Types of Ovariole

Two major kinds of ovarioles are classified on basis of presence of nurse cells and if present then position of these cells are considered. They also differ in the manner through which RNA and other nutrients are provided to developing oocyte.

- **Panoistic: Panoistic** (means all eggs) ovariole contain no special nurse cells. In **this**, germarium zone has simply oogonia, primary oocytes and pre-follicular tissue of mesoderm origin (Refer Figure 4.8). The follicular epithelium provides most of its nourishment to oocyte. It has selective genes amplification for ribosomal RNA in oocyte nucleus. Thus, it provides huge number of ribosomes which are essential for protein synthesis during development. The ring canals that bridge between germline cells are lacking in this type of ovariole. Panoistic ovarioles are considered as primitive type. Thus, these are present in insects, such as grasshopper, dragonflies, bristletails, stoneflies, termites and jumping bristletails.
- **Meroistic: Meroistic** is advanced kind of ovariole. In this, materials required for development of oocyte is provided by nurse cells or trophocytes whose genomes is increased through endomitosis. **Meroistic** (part eggs) ovariole contains stem cells, primary oocytes, pre-follicular tissue and **nurse cells** within zone of germarium.

Meroistic ovarioles are categorized into **telotrophic meroistic** and **polytrophic meroistic** (Refer Figure 4.8). In both kinds of meroistic ovarioles, nurse (nutritive) cells nourish oocyte with RNA, ribosomes and proteins during entire developmental process.

- o In **telotrophic** (or acrotrophic) ovariole, nurse cells situated at apex of ovariole (i.e., germarium). It feed oocyte through a nutritive (protoplasmic) cord as it descends alone. Examples are beetles and true bugs.
- o In **polytrophic** ovariole, nurse cells are closely associated with each oocyte and are enclosed within follicle. These ovarioles are present in booklice, louse and earwigs and holometabolous insects (except most beetles and fleas).

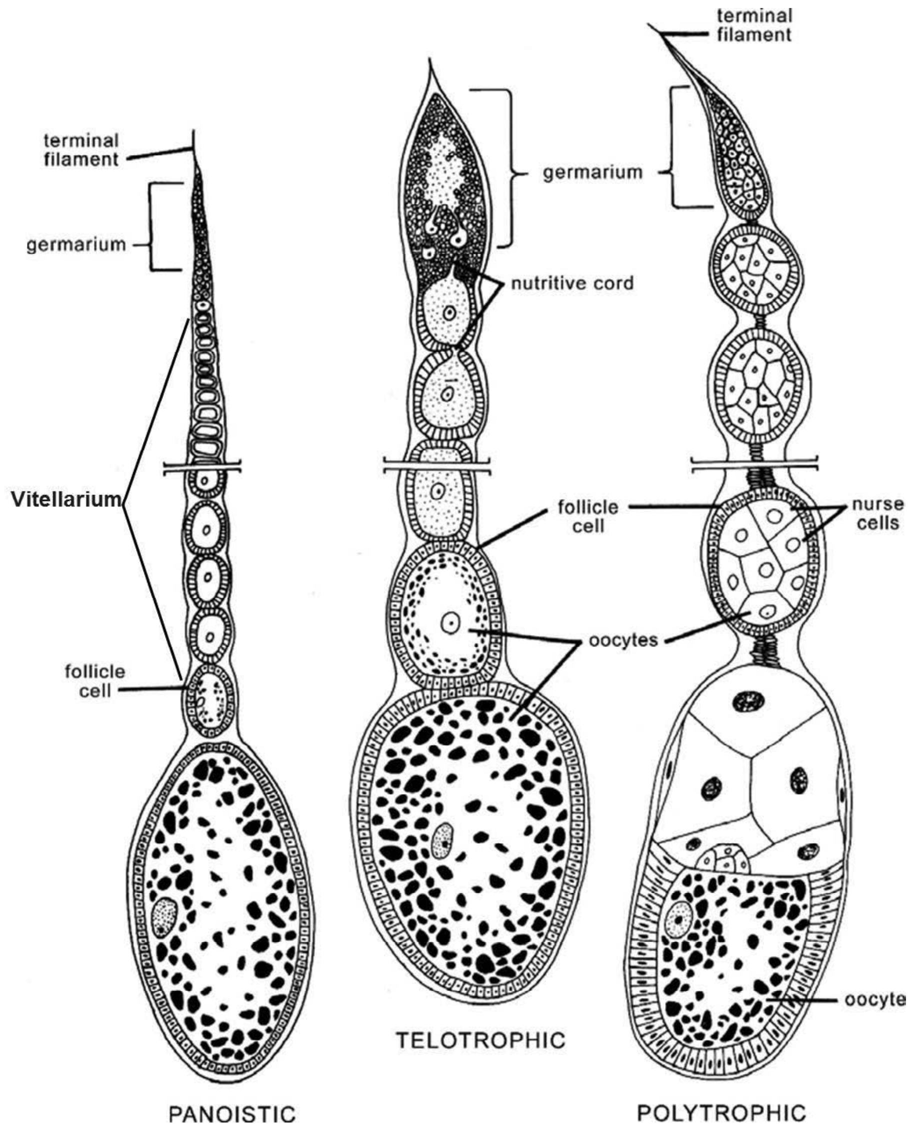

Fig. 4.8 Types of Insect Ovarioles; Telotrophic and Polytrophic are Subtypes of Meroistic Ovariole

2. Oviducts

Oviducts are tube like structure having epithelial wall. Generally, there are two lateral oviducts connect to a common (or median) oviduct. Lateral oviducts are thin-walled tubes that have an inner epithelial layer rest on basal lamina and outer layer of muscle. Common oviduct is lined with cuticle and is usually more muscular than lateral oviducts.

Modifications:

- Common oviduct leads at gonopore which is ventrally located on posterior end of 7th segment in Earwigs.
- In most other insects, common oviduct leads into a genital cavity invaginated above sternum of 8th segment of abdomen.

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- In some insects, the genital cavity develops as tubular structure. It is eventually a continuation of oviduct through 9th segment of abdomen. This continuation is known as vagina and its opening to outside is called as vulva.
- Vagina is often developed to produce a sac called as bursa copulatrix, for example bug, butterflies. It usually takes penis and eventually receives spermatophore during copulation.

3. Spermatheca

Usually single spermatheca is found in most female insects. It is used for storage of sperm that are received from male during copulation. Later these stored sperm are utilized for fertilization of eggs. Generally, spermatheca has a storage sac with a muscular duct leading to it. Spermatheca and duct with which it joins bursa are lined with cuticle. Epithelial cells of spermatheca become glandular. Secretions of these glands supply nutrients to the stored sperm. Also, they have role in sperm activation.

Modifications:

- Number of spermatheca may vary in insects. For example, there are 2 in darkling beetles and sandflies. Earwigs have 10 spermatheca that have a complex of four interconnecting spermathecal ducts.
- Spermatheca opens into genital cavity free from oviduct in case of Locusts and grasshopper.
- In other insects, where genital chamber becomes a vagina, spermathecal opening is inside and is being within oviduct.

4. Accessory Glands

Different accessory glands (also called collateral or colleterial glands) can be present and usually open into the bursa. Normally, there is one pair of glands, which secrete materials that form a protective coating around eggs or stick eggs to substrate during oviposition. Glands may produce antibacterial substances that coat eggs, toxic egg protectants and oviposition stimulating or oviposition-deterring pheromones. Accessory glands in female ascend from genital cavity or vagina. If these glands are absent in certain insects then walls of oviducts become glandular.

Modifications:

- In grasshoppers, glands called pseudocolleterial glands are anterior extensions of lateral oviducts.
- In bees, wasps and ants, the glands are single, not paired. It produces venom used in sting, secrete trail- or oviposition site-marking pheromones, or lubricate ovipositor valves.
- In many insects, such as cockroach, accessory glands form an ootheca that facilitate in protection of oviposited eggs.

Table 4.1 illustrates the difference between female and male reproductive organs of insects.

Table 4.1 *Comparison of Female and Male Reproductive Organs of Insects*

S.No.	Female Reproductive Organs	Male Reproductive Organs
1.	Paired ovaries composed of ovarioles (ovarian tubes).	Paired testes composed of follicles (testicular tubes).
2.	Paired oviducts (ducts leading from ovaries).	Paired vasa deferentia (ducts leading from testes).
3.	Bursa copulatrix (copulatory pouch) and spermatheca (sperm storage).	Seminal vesicles (sperm storage).
4.	Common (median) oviduct and vagina.	Median ejaculatory duct.
5.	Accessory glands (ectodermal origin: colleterial or cement glands).	Accessory glands (two types): i. Ectodermal Origin. ii. Mesodermal Origin.
6.	Ovipositor (if present).	Genitalia (if present): aedeagus and associated structures.

II. External Organs of Female Reproductive System

Organs concerned with mating and deposition of eggs are known collectively as external genitalia. These organs can be largely internal in female. Female external genitalia is simpler and less varied. Gonopore (opening) of common oviduct usually is concealed in an inflection of body wall that forms a cavity called as genital chamber. This chamber serves as a copulatory pouch during mating, and thus often is known as bursa copulatrix. Its external opening is the vulva. In many insects, vulva is narrow and genital chamber becomes an enclosed pouch or tube, referred to as vagina. In some insects, gonopore also works as ovipositor. In viviparous flies, anterior part of genital chamber is enlarged. This structure is called as uterus, in which larval development takes place.

III. Ova: Female Sex Cell

A. Structure of Ova

Ovum is genetically unique and is the **female gamete.** Followings are the structural and functional components of ovum:

- **Yolk:** Protoplasm of mature egg has plentiful yolk also called vitellus. Yolk nourishes the developing embryo. Yolk consists of globules of fat and protein that mostly cover the nucleus or germinal vesicle.
- **Eggshell:** It consists of three distinct layers which are formed during the late stage of oogenesis. These layers are vitelline membrane, wax layer and chorion.
- **Vitelline Membrane:** Egg or ova is coated by a delicate homogeneous sheet of vitelline membrane obtained from peripheral protoplasm of egg cell.
- **Chorion**: Vitelline membrane is covered by a hardened shell called as chorion. It is produced by follicular epithelium. Chorion have two layers namely exochorion and endochorion (Refer Figure 4.9). These two are joined through minute trabeculae.
- **Nucleus:** Egg cell's nucleus (haploid) lies within the yolk. It is usually close to one end of ovum.

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- **Cytoplasm:** Cell's **cytoplasm** is distributed in a thin band just inside vitelline membrane. At the time of oviposition, cytoplasm forms a bounding layer called as periplasm
- **Aeropyles:** Chorion is perforated by microscopic pores called as aeropyles. These allow respiratory exchange of oxygen and carbon dioxide with little loss of water.
- **Micropyle:** Micropyle is opening near anterior end of chorion. It serves as a passage for entry of sperm during **fertilization**.

Modifications:

- Chorion is thin and membranous in most endoparasitic wasps and thus able to stretch to a great degree with growth of contained embryo.
- Chorion is either rudimentary or absent in many viviparous insects.

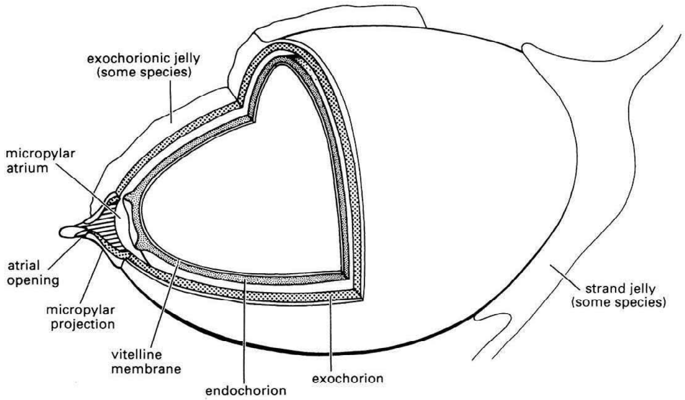

Fig. 4.9 *General Structure of a Libellulid Dragonfly Egg*

B. Formation of Ova: Oogenesis

Process for production of eggs or ova in female's body is called as **oogenesis**. In germarium zone of each ovariole, oocytes are formed from oogonia. In vitellarium zone, yolk is deposited in oocytes. Thus, these two zones of ovariole represent two phases of growth of oocyte.

- First phase is regulated directly through genome of oocyte and contains species-specific information. All materials whose synthesis is regulated by DNA of germ line are collectively called as **euplasm**.
- Second phase is chiefly regulated through genome outside of oocyte. It produces large collection of molecules which are involved in growth of embryo.

Germarium contains pre-follicular tissue, oogonial stem cells and their products. Oogonial stem cells are produced from primordial germ cells. When these stem cells undergo division, one of daughter cells becomes oogonial stem cell and other daughter cell forms a final oogonium. This final oogonium is known as cystocyte and develops into an oocyte.

In the Fruit fly (*Drosophila melanogaster*), oogenesis begins with four mitotic divisions starting from a single germ cell, producing a cyst of 16 cystocytes.

One of these cells will become oocyte and others 15 are supporting nurse cells. These mitotic divisions are exceptional because cytokinesis is incomplete, resulting in formation of cytoplasmic bridges known as ring canals that interconnect cystocytes (Refer Figure 4.10).

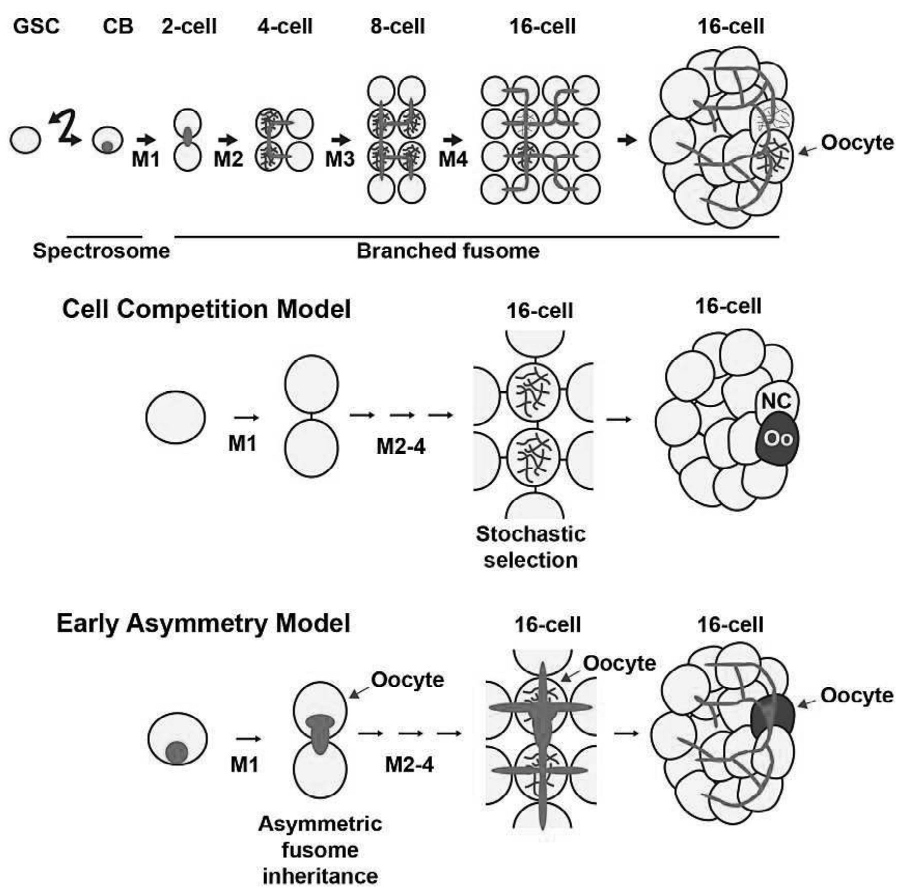

Fig. 4.10 *Oocyte Formation in Fruit Fly*

Following are the abbreviations used in above Figure 4.10; GSC: Germ Stem Cell, M1-M4: Mitotic Divisions, CB: Cystocyte or Cystoblast.

Reproductive Organs of Different Insects

1. Cockroach

Cockroach is dioecious, i.e., they have separate sexes. Sexual dimorphism is evident in both the internal reproductive organs and external morphology.

I. Male Reproductive System

Male reproductive organs include testes, vasa deferentia, ejaculatory duct, mushroom gland, seminal vesicles, phallic gland, genital pouch and external genitalia (Refer Figure 4.11). All these parts are located in abdomen. Mushroom gland and phallic glands form accessory reproductive glands.

- **Testes:** Male gonads are a pair of testes, lying embedded in fat body, one on either dorso-lateral side of 4^{th} to 6^{th} abdominal segments. Each testis is three-lobed and consists of several (30-40) small whitish transparent follicles arranged in a longitudinal series around a narrow, delicate vas deferens, into which they discharge sperms. In adult cockroach, testes become non-functional and greatly reduced in size.

- **Vasa Deferentia:** The paired vasa deferentia, one from each testis, run posteriorly and downwards to open into ejaculatory duct.
- **Ejaculatory Duct:** It is a single, median and muscular duct that extends posteriorly and opens into the genital pouch through male genital pore. Genital pore is lying below anus and between 9th and 10th sterna. Glandular wall of ejaculatory duct secretes middle layer of spermatophore.
- **Mushroom Gland:** Junction of two vasa deferentia and ejaculatory duct is surrounded by an elaborate mushroom gland consisting of numerous compact, finger like blind tubules arranged in two distinct groups and opening into anterior part of ejaculatory duct.
    - o **Utriculi Majores:** These are long, slender and peripheral tubules. Their secretion forms inner layer of spermatophore.
    - o **Utriculi Breviores:** These are short tubules forming bulk of mushroom gland. Their secretion nourishes sperms.
- **Seminal Vesicles:** Seminal vesicles are two groups of numerous small glistening white sacs. It present on ventral surface of anterior part of ejaculatory duct. It serves to store sperms. Seminal vesicles can be distinguished from utriculi breviores of mushroom gland by their slightly larger size and more opaque whiteness.
- **Phallic or Conglobate Gland:** It is a large, multilobed, leaf-like or club-shaped gland. It is present below ejaculatory duct and reaching anteriorly up to 5th abdominal segment. Its narrow duct opens into genital pouch by side of male genital pore. Phallic gland secretes outer layer of spermatophore.
- **Genital Pouch or Chamber**: It lies at hind end of abdomen covered dorsally by 9th and 10th terga and ventrally by 9th sternum. It contains dorsal anus, ventral male genital pore and gonapophyses.
- **External Genitalia or Gonapophyses:** In genital pouch, surrounding male genital pore, are present phallic organs. It helps in copulation. These have three small irregular chitinous plates namely right, left and ventral phallomeres.
    - o **Right Phallomere:** It is mid-dorsal in position. It has two chitinous but membranous horizontal opposing plates and a broad serrate lobe with a saw- toothed edge and two large teeth, and at its posterior side it has a sickle-shaped hook.
    - o **Left Phallomere:** It has a broad base from which several structures arise, on the extreme left is a long slender arm with a curved hook called titillator, next to the titillator is a shorter and broader arm ending in a black hammer-like head called pseudopenis. Close to the pseudopenis are three small soft lobes, one of which bears a hook and is called an asperate lobe. The duct of the phallic gland traverses the left phallomere and opens between the asperate lobe and pseudopenis.

o **Ventral Phallomere:** It is very simple in structure and lies partly below the right phallomere. It has a large brown plate and bears the male gonopore

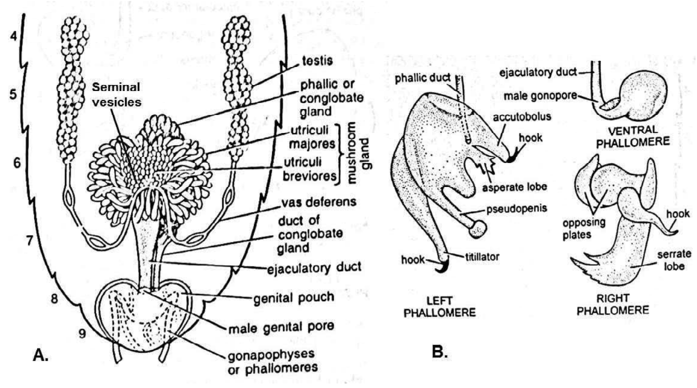

Fig. 4.11 *A. Male Reproductive Organs in Dorsal View; and B. Male Gonapophyses of Cockroach*

II. Female Reproductive System

Female reproductive organs of Cockroach contain ovaries, oviducts and vagina spermatheca, collaterial gland, genital pouch and external genitalia (Refer Figure 4.12). These are present in abdomen.

- **Ovaries:** A pair of yellow-coloured ovaries lies in 2nd to 6th abdominal segments, one on either side of hindgut and embedded in fat bodies. Each ovary contains eight elongated, tapering and beaded blind tubes called ovarian tubules or ovarioles. Each ovariole has linear series of ova in various stages of development. Each ovariole divided into regions namely germarium, vitellarium and terminal filaments. Anterior region of ovariole is germarium having immature ova in early stages of egg-formation. Posterior region of ovariole is vitellarium having maturing eggs. Anterior tapering apical ends of ovariole called terminal filaments. Terminal filaments of ovarioles of each ovary join to form a single thread called suspensory ligament.
- **Oviducts and Vagina:** Posteriorly, all the ovarioles of an ovary join to form a short and broad lateral oviduct. Two lateral oviducts in their turn unite in 7th segment to form a very short median common oviduct. Its posterior wider part is known as vagina which is formed as an invagination of body wall. It opens into a large genital pouch by vertical slit-like vulva or female genital pore on 8th sternum.
- **Spermatheca:** Spermatheca are a pair of club-shaped, unequal-sized, one spermathecae being larger than the other, structures. Both the spermathecae unite to form a short common duct which opens into the genital chamber on a small spermathecal papilla. Some workers claim that there is a single spermatheca and it has a lateral caecum.
- **Accessory or Collaterial Gland:** A pair of much branched accessory or collaterial gland lies behind and above ovaries. Left gland is opaque and more developed and right one is transparent and less developed. The two

open into genital pouch through two separate openings, lying close together, little behind and above spermathecal opening. Secretion of two collaterial glands forms hard egg-case or ootheca around groups of eggs.

- **Genital Pouch:** Genital pouch is located at posterior end of abdomen. Seventh sternum is large, boat-shaped and split behind into two apical lobes or gynovalvular plates. These plates form lateral, ventral and posterior limits are formed respectively by 8^{th} and 9^{th} sterna. Genital pouch can be divided into two parts. Its smaller anterior part has female gonopore. Pores of spermatheca and collaterial glands are called as genital atrium. Whereas its larger posterior part called as vestibulum in which ootheca is produced.
- **External Genitalia:** External genitalia lie concealed inside the gynatrium. They consist of an ovipositor formed by two gonapophyses. The ovipositor lies above and behind the gonopore, it is short and has three pairs of elongated processes, a pair of long thick arms lying dorsally and enclosing two pairs of slender tapering arms.

These two pairs of arms arise from a common base and they constitute the posterior gonapophyses, they belong to the 9^{th} abdominal segment and are joined to the 9^{th} tergum.

The third pair of arms of the ovipositor is large, they converge and meet posteriorly lying below the posterior gonapophyses and constitute the anterior gonapophyses. These belong to the 8th abdominal segment and are attached to the outer margins of 8^{th} tergum. The ovipositor is used only to conduct fertilised eggs to the oothecal chamber.

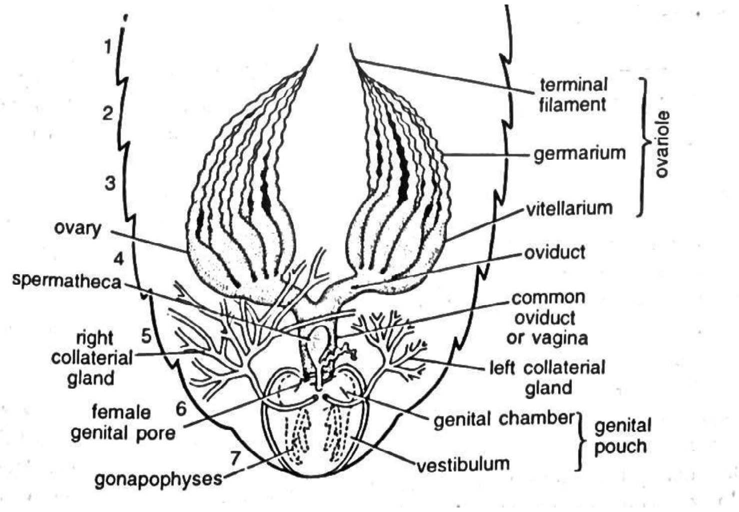

Fig. 4.12 *Female Reproductive Organs in Dorsal View in Cockroach*

2. Honey Bee

Drone: Reproductive organs of drone (male) are consist of testes, vasa deferentia, seminal vesicles, accessory or mucous glands, ejaculatory duct and penis (Refer Figure 4.13). Testes are a pair of yellowish, small, triangular lobes. Each testis consists of a large number of small tubules opening into a collecting reservoir at end of vas deferens. Spermatozoa pass down through coiled vas deferens and collect in saclike enlargement of this duct, which forms seminal vesicles. In mature adult drone, elongate sacs of seminal vesicles are densely packed with active spermatozoa, while testes that produced them become rudimentary. Each seminal vesicles opens by a short duct into base of accessory mucous gland of same side. Accessory mucous glands are two large sacs and are filled with a thick, white, homogeneous, finely granular liquid. This liquid is mixed with spermatozoa when these sperms are discharged. Mucous glands open at bases into single median ejaculatory duct which opens into anterior end of penis.

Queen and Worker Bee: Reproductive system of female bee contains a pair of ovaries, paired lateral oviducts and a median common oviduct. The ovaries of queen bee form two large gourd-shaped masses. There are more than hundreds ovarioles per ovary are in case of queen bee whereas this is rarely more than five in the case of worker bee. The common oviduct opens into the vagina which opens at the base of the sting. Posterior part of vagina is very large and forms a bursa copulatrix. A sperm receptacle called as spermatheca (storage sac for sperm) opens by a short duct into the vagina in the case of queen bee. Spermatheca made of a globular seminal sac and a pair of tubular accessory glands. When a queen bee mates with several drones, the sperms of all drones are stored in spermatheca. Later on it is used for fertilizing the ova as and when required. In bee, the two poison glands namely venom gland and Dufour gland into base of sting (Refer Figure 4.14).

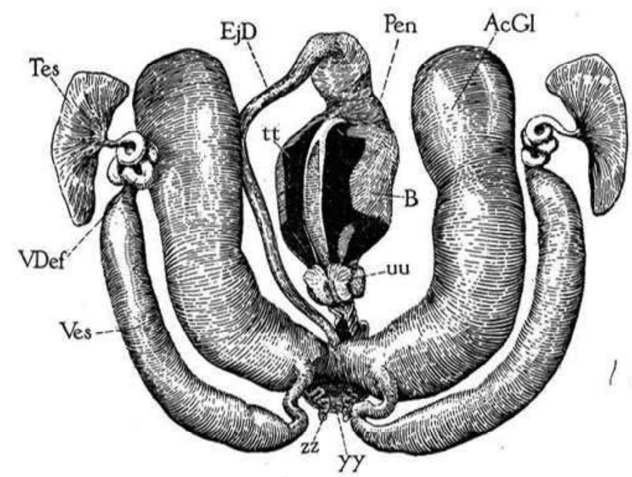

***Fig. 4.13** Dorsal View of Reproductive Organs in Male Drone Honey Bee*

Following are the abbreviations used in above Figure 4.13: Tes: Testes, VDef: Vasa Differentia, Ves: Seminal Vesicles, B: Bulb (bulb of penis or of sheath of sting), Pen: Penis, EjD: Ejaculatory Duct, AcGl: Accessory (Mucous) Gland, tt: Dorsal plates of bulb of penis, uu: Fimbriated dorsal lobes of penis at base of bulb, yy: Basal pouch of penis, zz: Copulatory sacs of penis.

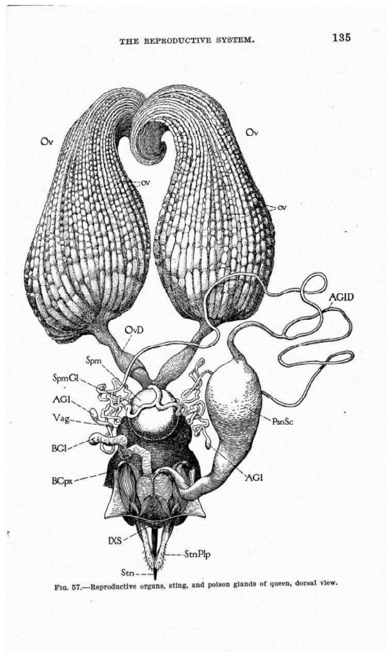

Fig. 4.14 Dorsal View of Reproductive Organs, Sting, and Poison Glands of Queen Honey Bee

Following are the abbreviations used in above Figure 4.14: Ov: Ovaries, ov: Ovarioles, OvD: Oviduct, Spm: Spermatheca, SpmGl: Accessory Glands, Vag: Vagina, BCpx: Bursa Copulatrix, AGI: Acid (venom) gland of sting, BGl: Dafour gland, AGlD: Duct of sting acid gland, PsnSc: Opening into poison sac, BGl: Alkaline gland of sting, Stn: Sting, StnPlp: Palpus like appendages of the sting, equivalent to the third gonapophyses.

Check Your Progress

1. How does reproduction in insects occur?
2. Name the parts of insect reproductive system.
3. What are the names of male reproductive system in insects?
4. What are testis in insects?
5. Write a short note on seminal vesicles in insects.
6. What is the structure of sperm?
7. Define the term spermatogenesis.
8. Name the parts of female reproductive organs in insects.
9. What are ovarioles?

4.3 PHYSIOLOGY OF REPRODUCTION

Most insects reproduce sexually and also are dioecious that is male and female insects are separate. Sexual reproduction involves several physiological events, such as mating of insects and sperm transfer, egg (oocyte) development and egg

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fertilization (Refer Figure 4.15).

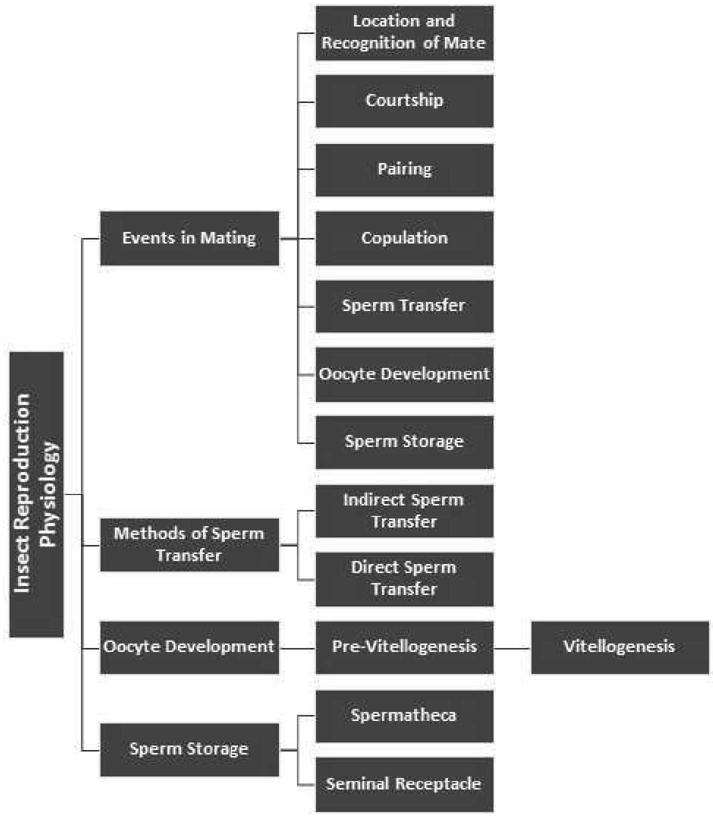

Fig. 4.15 *Features of Reproduction Physiology in Insects*

4.3.1 Mating

Mating behaviour of most insects can be subdivided into four parts. These parts are i. Location and recognition of a mate, ii. Courtship, iii. Pairing and iv. Copulation. Main function of mating behaviour is to ensure the transfer of sperm from male to female.

1. Location and Recognition of Mate

A pre-requisite to internal fertilization for nearly all terrestrial animals including insects is the coming together of male and female adults so that sperm can be transferred directly into a female's reproductive tract.

i. **Apterygote (Wingless) Insects:** In some apterygote (wingless) insects, indirect sperm transfer takes place. In springtails, males deposit packages of sperm onto substrate, but at that time females are not present in surrounding area. Females find sperm packages by chance and take them up into their reproductive system. In silverfish, droplets of sperm are placed on substrate, but only when a female is there.

ii. **Pterygote (Winged) Insects:** In pterygote (winged) insects, a range of stimuli can be used alone or in combination to locate a mate. These can be visual, olfactory, auditory, or tactile stimuli.

   a. **Visual Cues:** Visual cues are used mostly by many diurnal species. Movement, color, form and size can attract one individual to another. For example:

- Many male flies are attracted randomly to dark objects of a given size range but do not make copulatory movements unless they receive correct tactile or chemical stimulus on contact.
- Male butterflies may fly toward objects whose movements follow a particular sequence and which are of a particular colour pattern. But final contact and attempts to mate depend on odour of object. Best-known nocturnal insects are fireflies. Both sexes/only females of fireflies can produce light by means of bioluminescent organs. In fireflies female glows continuously to attract males that land in her vicinity, then locate her exact position by olfaction.

b. **Pheromones:** Pheromones are most common signal used by insects in mate location. Volatile chemical attractants are both highly specific and capable of exerting their effect over a long distance. Pheromones are produced by females and are used by both diurnal and nocturnal insects.

c. **Auditory Stimuli**: Auditory stimuli exert their effect over some distance and are species-specific. In crickets, only males produce sounds that serve to orient and attract mates from distances up to 30 m. In grasshoppers, both males and females produce sounds that attract opposite sex. Males of some cicadas, katydids and crickets sing aggression songs that serve to keep the males a minimum distance apart. Thus spread the males over the widest area, thereby reducing interference during courtship and mating.

2. Courtship

In some insects, recognition and attraction is immediately followed by copulation. But in other species, process of courtship occurs before copulation. Courtship is a close-range and intersexual activity which encourages sexual receptivity before and during mating. During an act of courtship, one or both sexes of insects influence each other's behaviour in order to facilitate activities of mating, insemination and fertilization. Followings are variations in functions and mechanisms of courtship in different insects:

- Males of some locusts, damselflies and monarch butterfly will mount or grasp an available female. When opportunity arises, male may not mate for some time until female is about to oviposit. This phenomenon is known as pre-copulatory mate guarding. It ensures that mounted male's sperm will be used to fertilize eggs.
- In insects where a female is normally aggressive, courtship serves to appease her so that she becomes willing to copulate. A well-known example of such appeasement is found in Dance Flies so-called as male has an elaborate courtship dance in which he presents female with a silken ball.
- Males of many species use liquid or pheromonal secretions as aphrodisiacs to pacify their partner. In many male grasshoppers, cockroaches and beetles, glands on thorax, head, antennae, palps, or elytra release a secretion that pacifies female when ingested. Many male butterflies and moths produce

pheromones that act as arrestants. It inhibits female's movement and stimulating her to adopt mating position.

- Courtship is very important in sexual selection that is choice of a mate by female. In firefly, male flash duration and size of lantern (flashing apparatus) are correlated with size of male's spermatophore. Females, which do not feed as adults, prefer males with longer flashes and larger lanterns. Thus, female gain benefits of a larger spermatophore, including more sperm and greater nutrient content.

3. Pairing

In this event, male holds female with his feet. Followings are examples of insects having different pairing position:

- Yellow fever mosquitoes lie with their ventral sides and male grasps hind legs of female. With his middle and hind legs, male push up the female abdomen until genital interaction is happened. Afterwards his middle legs hook onto the female wings but his hind legs remain free.
- In male damselflies, way of holding female is different. Firstly, male adult holds female thorax through his second and third pairs of legs. While first pair legs of male touch basal parts of her antennae. Later male adult flexes his abdomen forwards and fits two pairs of claspers (situated on segment 10 of his abdomen) into position on her head or thorax. In this position, he lets go with his legs and the two adults fly off 'in tandem'.

4. Copulation

Copulation is the reproductive or mating act in which male reproductive organ, for example penis enters female reproductive organ, for example vagina. *Copulation* usually includes mounting, *intromission* (insertion of penis into vagina), and sperm discharge in to female insect. Copulation performed just after insects become paired or there can be some interval before they copulate. Followings are features of insects for copulation:

i. **Receptivity Factors:** Receptivity (willingness of a female to copulate) depends not only on a male's efforts to seduce her but also on female's physiological state.
   - Many females mate only once or a few times and after mating become unreceptive to males for some time due to presence of semen in spermatheca.
   - In other insects, inhibition is pheromonal that is seminal fluid has receptivity-inhibiting substance. This acts either directly or by causing spermatheca to liberate a hormone into haemolymph. Thus, by acting on the brain, female becomes unreceptive.

ii. **Initiation of Copulation:** Insects have some mechanisms to initiate copulations, for example:
   - **Large Cockroach:** The female climbs on back of male in cockroach. In this insect, signal that adults are in suitable position for copulation arises from mechanosensitive hairs on his first abdominal tergite. Hairs are stimulated when she efforts to feed on a secretion released by glands

adjacent to hairs and this event happens when female is properly positioned for male to copulate.

- **Dragonflies:** Copulation includes activities, such as male bending his abdomen so as to the female head touches his accessory genitalia. Eventually she brings her abdomen forwards below her body so that create contact with his accessory genitalia.

iii. Duration of Copulation: Duration of copulation, pre-copulation and post-copulation varies in insects as follows:

- **Copulation Period:** In mosquitoes, copulation completes within few seconds, whereas seed bugs remain coupled for five hours, for 8–10 hours in Locusts and for up to 60 hours in tree locusts. Transfer of sperm happens faster than this, for example sperm reach spermatheca within two hours of start of copulation in Locust.
- **Pre-Copulation Period:** Many insects settle before copulating and the process can last from a few minutes to more than hour. During this time male removes sperm previously present in spermatheca to minimize the last sperm paternity (also called sperm precedence). Whereas, sperm transfer takes only a few seconds. Examples are butterflies and moths.
- **Post-Copulation Period:** Duration of coupling after insemination (sperm transfer) depends on male density in population. In green stink bug, copulation continues for 1-2 days if the population contain majority of females. While, this become prolonged for up to seven days when majority of males are present. Extended copulations help to protect against further mating by the female and thus guard the copulating male from sperm competition.

4.3.2 Transfer of Sperm

Process of sperm transfer by male to female reproductive organs during copulation is called as **insemination**. Methods of sperm transferred by male in female vary in different insects, which are explained below:

- **Indirect Sperm Transfer:** As discussed earlier (under heading-location and recognition of mate), indirect sperm transfer occurs in some apterygote insects. In this method, male drops sperm packages or spermatophore on ground which later picked up by female.
- **Direct Sperm Transfer:** In pterygote insects, sperm is transferred during copulation directly to female reproductive organ. It occurs in three ways: i. sperm transfer with spermatophore, ii. sperm transfer without spermatophore; and iii. heamocoelic insemination. Followings are the details about these ways:

I. Sperm Transfer with Spermatophore

Sperm are enclosed in a special structure called spermatophore, which can be formed some time before copulation (for example in Crickets) or more common as copulation proceeds. In this method, spermatophore is introduced into bursa copulatrix of female from where sperm move to spermatheca.

i. Structure of Spermatophore

- In springtails (apterygota), male drops spermatophores on ground regardless of presence of female. Spermatophore consists of sperm enclosing droplet, lack any adjacent membrane, attached on top of a stalk that can about 500 mm high.
- In pterygote insects, spermatophores are transferred directly from male to female body. When spermatophore (Refer Figure 4.16**)** is formed outside of female, one or two sperm sacs embedded in a gelatinous proteinaceous mass known as spermatophylax.

ii. Production of Spermatophore

Spermatophore is made up from secretions by accessory glands of male's reproductive system. When these glands are absent or reduced then secretions from glands in ejaculatory duct (or the simplex in butterflies) are involved. Secretions from different glands or different cells within a gland are produced in series to form different parts of spermatophore.

There are four general methods of spermatophore formation. First two methods are male-determined and remaining two methods are female-determined. Details of these methods are as follows:

- The most primitive method or first male-determined method found in many orthopteroid insects, such as grasshoppers and locusts. Spermatophore is complex and formed either at anterior end of ejaculatory duct or within male copulatory organ. After transfer to a female, spermatophore is usually held between her external genital plates and only it's anterior, tube like portion enters vagina or bursa.
- In second male-determined method, spermatophore has a less complex structure and is formed within a special spermatophore sac of copulatory organ. Thin-walled sac is turned into bursa. Therefore, it determines final shape and size of spermatophore. After spermatophore formation, sac is removed. Assassin bugs*,* some beetles, and some flies form spermatophores in this way.
- First female-determined methods are present in caddisflies, butterflies, some flies, some beetles, and a few wasps. Male accessory gland secretions empty directly into vagina or bursa in a sequence. It is either before or after transfer of sperm which they encapsulate. Spermatophore takes up shape of genital duct.
- Spermatophore produced by second female-determined method is slightest complex. Male accessory gland secretions are produced concurrently with or immediately after sperm transfer and often do not encapsulate the sperm. Instead, it hardens to form a mating plug that prevents backflow and loss of semen (and also, re-mating). This method is seen in mosquitoes, honey bee and some butterflies.

Spermatophore Production in Butterflies and Moths

Spermatophore is formed completely within female ducts after start of copulation. Various glands in female secrete starting from simplex and function in a sequence.

Aedeagus protrudes into bursa copulatrix and secretion from lower region of simplex form a pearly body and wall of spermatophore. Partially mixed secretions of seminal vesicle, sperm and seminal fluid form inner matrix of spermatophore. Secretion of lower parts of accessory glands produces outer matrix. At last, secretions from ends of glands produce spermatophragma that blocks duct of bursa copulatrix (Refer Figure 4.16).

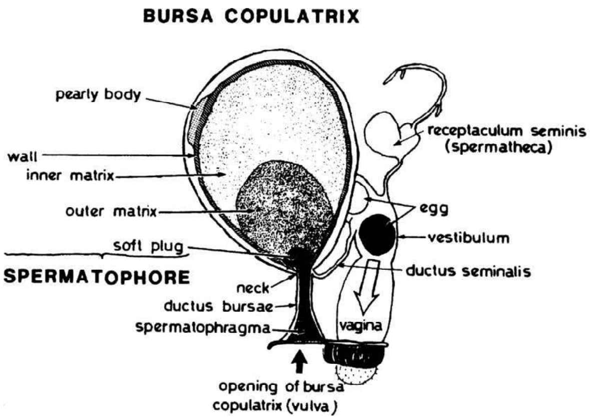

Fig. 4.16 *Spermatophore Completely Formed within Bursa Copulatrix in Female Silk Moth after Mating*

iii. Sperm Transfer from Spermatophore to Spermatheca

After transfer of spermatophore, sperm move into spermatheca in which they are stored. Escape of sperm from spermatophore to spermatheca varies with insects. Followings are the various methods:

- In some insects, sperms escape from sperm sac through a pore.
- In other insects, sperm sac is entirely bounded within spermatophore so they escape when spermatophore ruptures.
- In butterflies, inner lining of bursa copulatrix have spines or bears a toothed plate called signum dentatum. Muscles are attached to signum dentatum. Spermatophore is slowly scraped by movements of spines until it is broken up to release sperm.
- In many insects, spermatophore is deposited in bursa copulatrix of female and transfer of sperm to spermatheca takes place through contractions of female ducts, for example assassin bugs.

iv. Fate of Spermatophore

Females of insects eject spermatophore sometime after insemination. Proteolytic enzymes in some insects facilitate digestion of spermatophore, for example butterflies and caddisflies. In wax moth, digestion is completed in ten days, but neck of spermatophore persists yet. Spermatophore of locusts ruptured after two sexes get separated.

II. Sperm Transfer without Spermatophore

In insects where spermatophores are not used in insemination, sperm transferred directly into spermatheca through penis. In such insects, penis is thin-walled, long and flagelliform. Penis can be erected by hydrostatic pressure, either of haemolymph or of fluid contained within a special reservoir at ejaculatory duct. It extends far into genital tract of female and terminates near to spermatheca. This type of direct sperm transfer found in some flies, dragonflies, beetles, scorpionflies and wasps. Detailed processes of direct sperm transfer in mosquitoes and dragonflies are given below,

Direct Sperm Transfer in Mosquitoes: In yellow fever mosquitoes, paraprocts (sclerites near anus) inflate female genital opening, whereas aedeagus is erected by activity of muscles attached to apodemes. Aedeagus enters just into female opening where it is held by spines associated with valve of spermatheca. A pool of fluid from accessory glands is taken along ejaculatory duct and into female by contractions of glands. Sperm are injected into pool by contractions of seminal vesicles. Therefore a bulk of semen is placed inside female and from where eventually sperm are transferred to spermatheca.

Direct Sperm Transfer in Dragonflies: Dragonflies and damselflies have a unique mode of sperm transfer. Male copulatory organ is a tubular structure formed on third abdominal sternum. Before mating, a male transfers sperm to copulatory organ by coiling abdomen ventrally. Mating occurs during flight, female held around head or prothorax by male's terminal claspers. This brings tip of her abdomen into contact with copulatory organ (Refer Figure 4.17). Male's copulatory organ is also equipped with horns and/or spines. Therefore these insects not only transfer sperm to female but first remove sperm deposited in a previous mating.

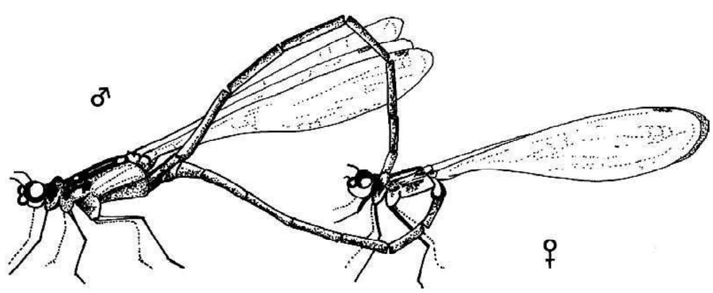

Fig. 4.17 *Copulating Damselflies*

III. Haemocoelic Insemination

This most unusual form of insemination is found in bedbugs, capsid bugs (*Miridae*) and twisted-wing parasites (*Strepsiptera*). It involves injection of sperm into body cavity (haemocoel) of female from which they migrate to specialized storage sites called seminal concepticals (conceptacula seminales) near to oviducts. Thus, bed bugs do not have spermatheca instead they have seminal concepticals. Sperm move from seminal concepticals to oviducts and fertilize eggs in ovaries.

Followings are the evolutionary sequence of development of haemocoelic insemination in these insects:

- Primitively, penis is placed in vagina but penetrates its wall, thereby injecting semen into body cavity.
- At a more advanced stage, penis penetrates integument, but not at any predefined site and sperm are still injected into haemolymph.

- Next, site of penetration becomes fixed and below it a special structure called spermalege, develops to receive sperm. But, sperm must still migrate via haemolymph to conceptacula seminales.
- At most advanced level, insemination into spermalege takes place. Sperm move to conceptacula along solid core of cells. Spermalege is unique to bed bugs and is an organ filled with haemocytes that lies in body cavity at site of haemocoelic insemination (Refer Figure 4.18).

Functional Significance: In all forms of haemocoelic insemination a proportion of sperm are phagocytosed either by haemocytes or by cells of spermalege. In this way, in Cimicoidea haemocoelic insemination is a method of providing nutrients to female. It enables her to survive for longer periods in absence of suitable food. This occurs because many Cimicoidea are semiparasitic or parasitic and chances of locating a host are slight.

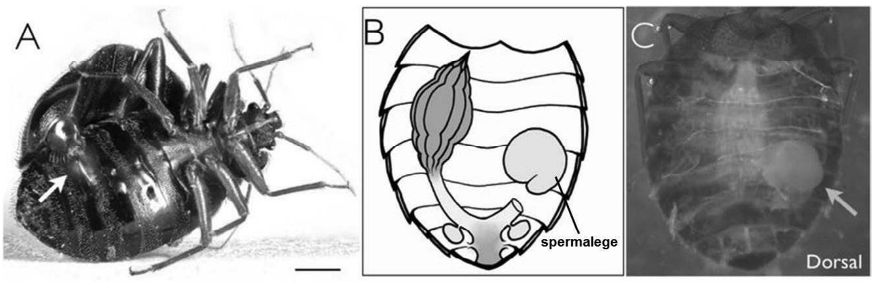

Fig. 4.18 *A. Ventral View of Bed Bugs during Haemocoelic Insemination, B. Dorsal View of Reproductive System of Female Bed Bug; and C. Dorsal View of Inside of Female's Abdomen*

In above Figure 4.18 A. shows ventral view of bed bugs during haemocoelic insemination in which arrow indicates point at which male has inserted his intromittent organ into specialized groove in female's abdominal wall; B. shows schematic of reproductive system of female bed bug (dorsal view); and C. shows dorsal view of inside of female's abdomen.

Other Mating Effects

Sperm transfer involves lubrication that is provided by seminal fluids and spermatophore formed in some insects. Secretions of male reproductive tract perform these functions. Secretions are involved with final maturation of sperm in female. Also, secretions provide energy for sperm maintenance and maintain female physiology. The seminal fluid chemicals can induce various post-mating physiological behaviour of female by entering her haemolymph and acting on her nervous and sometime endocrine system. Two major effects are: (i) induction of oviposition i.e. egg-laying by increasing ovulation and/or (ii) suppression of sexual receptivity to reduce her ability to re-mate.

4.3.3 Vitellogenesis

Copulation initiates oocyte development, oviposition and sometimes inhibition of sexual receptivity in female. It occurs through enzymes or peptides passed to female reproductive system from secretions of male accessory gland. Successful mating in insects leads to fertilization of ova and then triggers embryogenesis via egg activation. Egg activation is process oocyte development and growth. Oocyte growth and development involves basically two processes namely, pre-vitellogenesis and vitellogenesis.

- **Pre-Vitellogenesis:** Pre-vitellogenesis is a process where there is an increase in nuclear and cytoplasmic material in oocyte with no addition of yolk.
- **Vitellogenesis:** Vitellogenesis is a process of synthesis and deposition of large amount of yolk in oocyte. Insect's eggs are both microlecithal and centrolecithal types. Thus, insect eggs have massive yolk that occupies center of egg and cytoplasm forms a thin peripheral layer around yolk. Chemically yolk is lipoprotein composed of proteins, phospholipids and neutral fats along with a small amount of glycogen. Functions, composition and formation of yolk in details are discussed as follows:

i. Functions of Yolk

- Yolk is also called as deutoplasm, is nutrient-bearing portion of egg and supply food to embryo at the earliest stages of development.
- Major proteins are stored in the yolk of developing oocytes that provide a nutritional store for utilization during embryogenesis.
- Yolk supplies energy to developing embryo.
- It provides material for synthesis of those substances that are required for elaboration of embryonic body.
- Amount of yolk in an egg cell affects developmental processes that follow fertilization. It has important influence on:
  - The size of egg,
  - The differentiation of ooplasm,
  - The pattern of cleavage,
  - The early morphogenetic movements of blastomeres during gastrulation; and
  - The type of development (direct or indirect).

ii. Composition of Yolk

Less than 10% part of the total oocyte typically constitutes the euplasm (genomic materials). Rest of the 90% part of oocyte is yolk that mainly consists of lipids and proteins. About 40% of dry weight of terminal oocyte contains lipids and main lipid is triacylglycerol. Protein content of yolk is almost equal to lipid content and 60-90% of yolk proteins are produced from vitellogenins.

iii. Formation of Yolk

Nurse cells (trophocytes) and ovarian follicle cells in ovariole are involved with development of oocytes. These cells provide nutrients to developing oocytes. As oocyte is growing comparatively at slow pace, sequentially there is a period of rapid yolk deposition. It occurs in terminal oocyte of each ovariole and results in production of fully developed ova.

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Role of Vitellogenins in Yolk Synthesis: Vitellogenins are female specific Lipoglycoproteins (LGP) and are synthesized usually in fat body under influence of Juvenile Hormone (Refer Figure 4.19). These proteins move through haemolymph into oocytes by endocytosis and become vitellins. Chemical structure of vitellins is somewhat different from that of vitellogenins. Triglycerides as lipid bodies from follicle cells, nurse cells and/or fat body also are deposited in growing oocyte.

Synthesis of Yolk Proteins: Most of yolk protein is synthesized in fat body present near ovaries. Some insects also synthesize smaller quantities of other yolk proteins in addition to vitellogenins and lipophorin in fat body. Fat body of mosquitoes synthesizes pro-enzymes which are required for yolk metabolism during embryogenesis. These enzymes are known to be sequestered in oocyte outside yolk granules where vitellins are stored. These types of enzymes are also synthesized in several other insects.

Synthesis of Yolk Lipids: Majority of lipid which deposited in oocyte is synthesized in fat body. Less than 1% is produced in oocyte. Hornworm has 90% of lipid passed to oocyte through low-density lipophorins. The lipophorin delivers its lipids at membrane of oocyte and then is recycled. Rest of lipid derived from high-density lipophorin that is occupied by oocyte of hornworm. It forms the protein content of yolk.

Terminal Oocyte: Oocyte near to oviduct in each ovariole is called as terminal oocyte.

Fat Body: Fat body made up of storage cells and distributed throughout haemocoel (body cavity) near to epidermis, digestive organs and ovaries.

Lipophorin: *Lipophorin* is the major haemolymph protein responsible for lipid transport between tissues of insects.

iv. Deposition of Yolk in Oocyte

Deposition of yolk in oocytes takes place in lower and proximal part of ovariole that is vitellarium. It leads to a very fast increase in size of oocyte. In many insects deposition of yolk is mainly limited to terminal oocyte. Other oocytes do not grow in size until the first fully grown oocyte is released from ovariole into oviduct. The process of releasing oocyte into oviduct is called as ovulation.

As adult stage of butterflies, mayflies and stoneflies do not feed, process of yolk deposition, i.e., vitellogenesis takes place in late larval or pupal stage. But a period of oocyte maturation is required in adult of most of these insects before oocytes are prepared for ovulation.

Yolk deposition in oocyte is dependent on the pattern of nutrition. For example, blood-sucking insects like mosquitoes eat in discrete meals with long non-feeding periods. These insects give a batch of eggs following each meal. Quantity of eggs laid is proportional to quantity of blood eaten.

v. Hormonal Control of Vitellogenesis

In insects, vitellogenesis starts when the fat body stimulates the release of Juvenile Hormones (JH) and produces vitellogenin protein. Regulation of vitellogenesis varies with insects. JH secreted from corpora allata, ecdysteroids from prothoracic glands or the ovary, and brain neurohormones also called neuropeptides, for example Ovarian Ecdysteroidogenic Hormone (OEH) trigger production of vitellogenin with varying degrees in different insect species. In cockroaches, for example vitellogenesis can be stimulated by injection of juvenile hormone into immature females and mature males. In mosquitoes infected with *Plasmodium* (parasite), vitellogenesis can be affected by parasites to reduce fecundity (number of eggs).

Synthesis of vitellogenin is induced by JH that acts directly on fat body. Signal to induce juvenile hormone production is dependent on nutrient or mating status (Refer Figure 4.19). For example:

- In locusts, mating and certain food odours work through neuro-secretory cells located in brain so as to induce the production and release of juvenile hormone.
- In viviparous Beetle cockroach (*Diploptera punctata*), terminal oocytes are small ranges from 0.6 mm to 1.4 mm increases the rate of JH production. However big and fully developed oocytes cause inhibitory response that acts on the brain through the haemolymph. If an ootheca is formed, it induces mechanoreceptors in brood sac that inhibit synthesis of juvenile hormone through neural mechanism.

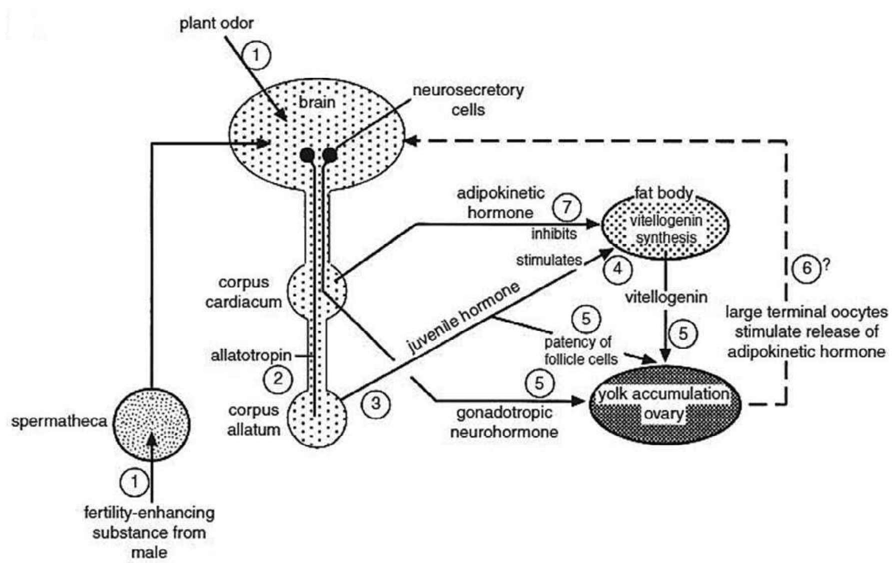

Fig. 4.19 *Hormonal Regulation of Vitellogenin Synthesis and Yolk Accumulation in Locust*

4.3.4 Sperm Storage

Female sperm storage is a process in which sperm transferred to a female during mating are temporarily retained within a specific part of reproductive tract before oocyte or egg, is fertilized.

I. Sperm Storing Organs

Females of many insects store sperm in spermatheca after she get sperm from one or more males during copulation. Some insects have additional sperm storing organ called as seminal receptacle. For example, Fruit fly (*Drosophila)* has single seminal receptacle is on ventral side and the paired spermathecae are on dorsal side of uterus. Two types of storage organs differ in morphology and in patterns of sperm storage.

- **Spermatheca:** In many insect orders, female contain a single spermatheca. Some flies are contain more, such as two or three spermatheca. Normally sperm continue to be viable in the spermatheca for a large duration, notably in honey bees, it is three or more years. When sperm are stored, secretions from her gland of spermatheca retain the sperm viability and vigour. Queen bee spermatheca contains about 5 million sperm, yet she produces on average at least 200,000 fertilized eggs during her 4 year life span. Thus, about 25 sperm per egg are released from spermatheca. There is a very precise control mechanism exists for sperm release.
- **Seminal Receptacle:** Seminal receptacle is a thin (5-20μm) blind-ended tube that is coiled against outer uterine wall. In fruit fly, seminal receptacle is more than 2 mm long. Numerically, the seminal receptacle in Fruit fly plays biggest role in sperm storage, retaining 65–80% of the stored sperm. Sperm are released almost exclusively from the seminal receptacle for the first several days after mating. Then, as the seminal receptacle sperm become depleted, sperm are released from the spermathecae.

II. Mechanisms of Storing Sperm

- **Female-Based Mechanisms:** Female-based mechanisms can include absorption of fluids from parts of her reproductive tract (called as hydraulics), contractions of uterus, contractions of sperm storage organs, restriction of sperm to particular regions of female reproductive tract, and/or factors secreted from within female reproductive tract.
- **Male-Based Mechanisms:** Male-based mechanisms are also important and can continue even after copulation is complete. These include sperm motility and seminal proteins. Sperm are motile when they are transferred to the female and when they are in storage.

III. Importance of Sperm Storage

- **Increases Fecundity and Fertility:** Sperm storage allows sperm from a given mating to be used long after the male and female have separated thus increasing female fertility.
- **Coordination of Ovulation Rate**: Sperm storage potentially allows coordination of ovulation rate with sperm release from storage. This prevents gamete wastage, which would occur when gametes are released at different times and unable to unite successfully.
- **Decrease Incidence of Polyspermy:** The coordination of sperm release and ovulation also decrease incidence of polyspermy that also wastes eggs and sperm because it results in nonviable fertilizations.
- **Fertility Insurance:** Sperm storage allows females to retain sperm for more than one male within her reproductive tract. This provides fertility insurance should any of the males be infertile or genetically incompatible with the female

- **Produce Different Genotypes:** Storing sperm from multiple males has the potential additional advantage for females of generating progeny with a broader range of different genotypes. When their habitat is spatially variable or changes over time, genetic diversity among offspring might be particularly advantageous for survival of at least some of the female's progeny.
- **Female Sperm Preference:** Finally, storing sperm from more than one male generates an opportunity for sperm competition and female sperm preference.
- **Decreases Tendency to Re-Mate:** After mating, females of many insects become unreceptive to courting males for several days.

Reproduction Physiology of Different Insects

1. Cockroach

Mating and Copulation

Sexually mature male and female cockroaches usually mate during night from March to September. During copulation, male transfers its spermatozoa in spermatophore directly into genital pouch of female. Mature female cockroach emits a volatile chemical called pheromone or sex attractant. This odour is detected by antennal chemoreceptors of male. In response, the sexually excited male raises its tegmina (forewings) by 45^o to 90^o and rapidly flutters its hindwings. In mating, first the male gets under female, extends his left hooked phallomere to insert into genital chamber of female. He clasps a small sclerite in front of ovipositor and then moves from below her. Both have an end to end position (Refer Figure 4.20A). The process of copulation lasts an hour or more after which male and female separate.

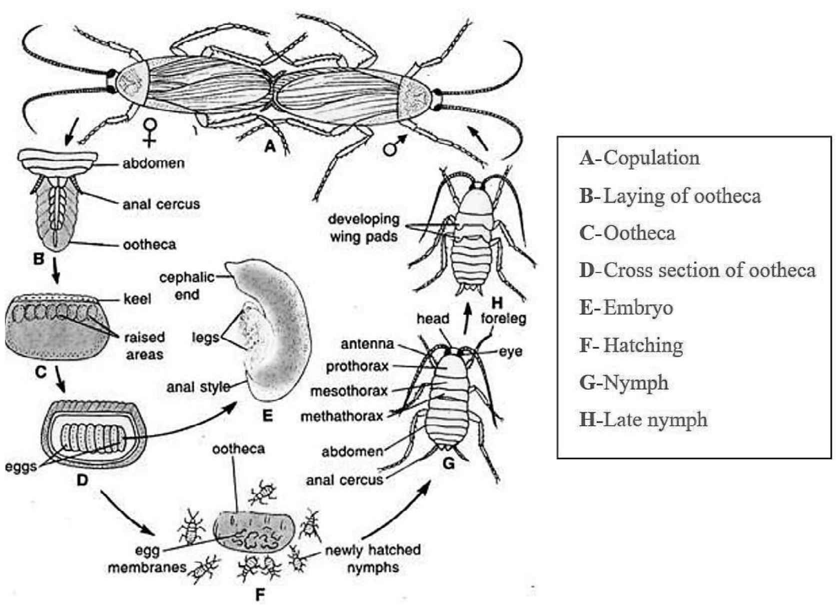

Fig. 4.20 *Reproduction in Cockroach*

The above Figure 4.20 shows reproduction in cockroach, in which A. shows copulation, B. shows laying of ootheca laying, C. shows ootheca, D. shows cross

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section of ootheca, E. shows embryo, F. shows hatching, G. shows nymph; and H. shows late nymph.

Sperm Transfer with Spermatophore

Spermatozoa produced in testes are stored in seminal vesicles of males. When cockroaches copulate, these sperm move into ejaculatory duct. In ejaculatory duct, sperm are mixed with a nourishing fluid secreted by utriculi breviores. At the same time, utriculi majores adds its secretion that hardens to form inner layer of spermatophore. Then glandular wall of ejaculatory duct secretes middle layer around inner layer of spermatophore. During copulation, two layered spermatophore is deposited into female genital pouch on spermathecal papilla. Here the secretion of phallic or conglobate gland forms its third layer (outer) layer.

Fully formed spermatophore is a three-layered tough and pear-shaped capsule about 1.5mm long (Refer Figure 4.21). Its central chamber contains spermatozoa in a spermatic fluid. Its capsule has a simple opening that comes in close contact with female spermathecal opening. Within 24 hours, sperms enter spermatheca where they remain stored until required. Empty spermatophore drops down.

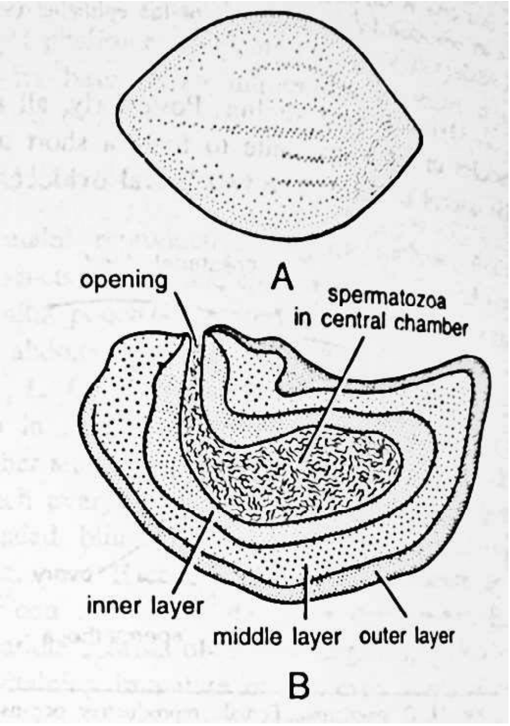

Fig. 4.21 *Spermatophore of Cockroach; A. Complete Form; and B. Cross Section*

2. Honey Bee

Copulation and Sperm Transfer

Only queen bee and drones have a fully developed reproductive system. Worker bees have an atrophic reproductive system. Events of copulation and sperm transfer in honey bee occur in following steps:

- After emergence, virgin queen leaves hive to find a drone congregation area. She mates usually with 8-12 drones in flight and in 15-30 m above ground, in temperatures higher than 20°C, with wind speed lower than 28 km/h and during afternoon hours.
- Aggregation (around thousand) of drones lazily flies within their congregation site awaiting arrival of a queen. As queen reaches congregation area, the nuptial flight begins. Drones fly slowly in a circular formation. Queen flies over the males and slowly descends. Some tens of males are attracted by both visual cues and queen's pheromones.
- Increasing their flight speed, the group of drones forms a comet tail. Copulation takes place in flight in few seconds. Drone clasps queen in a dorso-ventral position (Refer Figure 4.22.A) and put his endophallus directly into queen's sting chamber (Refer Figure 4.22D). In this way, drone mounts queen, inserts his endophallus in queen's vagina.
- Eversion (turning inside out) of endophallus occurs from haemostatic pressure caused by abdominal muscles. Sperm transfer (ejaculation) occurs into bulb portion of drone's endophallus prior to full eversion. Then semen is discharged through a small opening in bulb into queen's vagina during copulation. Mating lasts 5-18 minutes.
- During transfer of sperm, the copulatory apparatus is torn from body of male. Thus, male falls back (Refer Figure 4.22B) and endophallus remains attached to queen which becomes mating sign of queen. Another drones mounting later remove previous drone's endophallus and lose their own through matings. These emasculated drones die with their abdomens burst in this manner. At end of copulation, the drone falls to ground and dies either in minutes or hours (Refer Figure 4.22C).
- Over a few days, queen can have many nuptial flights. Finally, queen returns to colony, retaining last mating sign, which soon shrivels up and drops off. Queen stores entire spermatozoa in spermatheca and her gland secretes nutrients for survival of around 7,000,000 spermatozoa. A normally mated queen stores enough spermatozoa for 2 to 3 years of continuous egg laying.

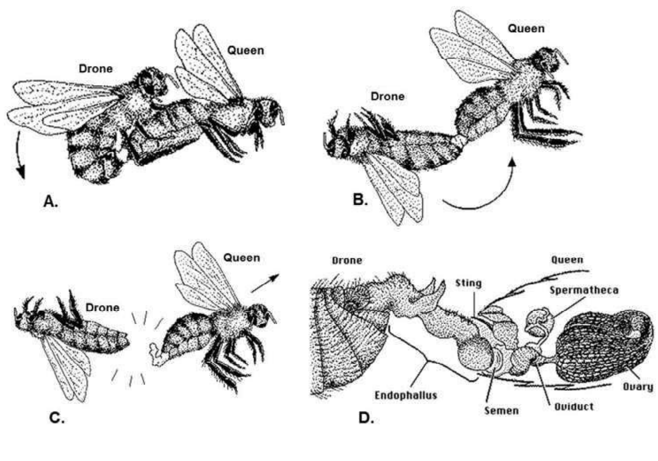

Fig.4.22 *A. Nuptial Flights in Honey Bee. B. Drone Falls Back, C. His Endophallus is Ripped Out of his Body and Remains Attached to Queen, D. Endophallus of Drone is Inserted into Sting Apparatus of Queen*

Check Your Progress

10. What are the different steps involved in sexual reproduction in insects?
11. In how many parts can mating behaviour of most insects divided?
12. Define the term pheromones.
13. What does copulation mean?
14. What is insemination?
15. Distinguish between pre-vitellogenesis and vitellogenesis.
16. Give the functions of yolk.

4.4 POLYEMBRYONY AND PARTHENOGENESIS

Most insect species are bisexual and females lay eggs that have large amount of yolk. Such insects are called oviparous. They lay eggs and later develop and hatch in outside environment. But, some insect species have following asexual and unusual modes of reproduction which are different from bisexual and oviparous insects:

1. Viviparity

In viviparity, female insect keep their fertilized eggs inside their genital tract until they develop into young ones and then these are laid.

Developing embryos obtain nourishment directly from female. These insects are called as viviparous. Hatched eggs or neonates (nymph or larvae) are come outside of body. Nourishment provided by female can be in addition to nutrients that are present in yolk of egg during oogenesis. Viviparous insects usually reproduce very small number of progeny than oviparous species. This can be due to small number of ovarioles present in female. For example, only two ovarioles per ovary are present in biting flies and tsetse flies, while 70 ovarioles per ovary are found in oviparous insect of related species, for example houseflies.

Pseudoplacental Viviparity: Some aphids, Booklice (*Psocoptera*) and Earwig (*Dermaptera*) have pseudoplacental viviparity. Eggs of these insects have little or no yolk and lack chorion. They develop within ovariole, where follicle cells supply at least some nourishment to the embryo. In Earwig, follicle cells adjacent to anterior and posterior ends of an oocyte proliferate and become connected with embryonic membranes forming pseudoplacentae. Later, follicle cells degenerate as they are supplying nutrients to developing embryo (Refer Figure 4.23).

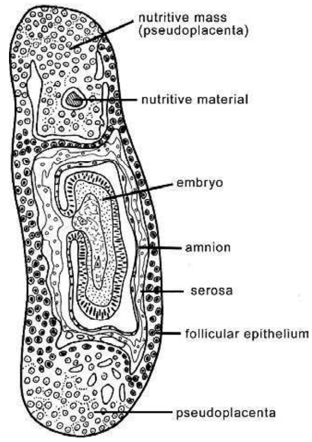

Fig. 4.23 *L.S. through Ovarian Follicle of Earwig to show Pseudoplacentae*

2. Ovoviviparity

In ovoviviparity, female insects keep their eggs in reproductive tract until before eggs are ready to hatch. These insects are called ovoviviparous. Their eggs undergo partial embryogenesis in female parent body and then they are laid. All the nourishment for embryo obtains from yolk in egg. These insects produce fewer eggs and each acquires more yolk. Thus, larvae can hatch at more advanced stages of development.

Ovoviviparity in Tachinid Flies: Ovoviviparity is seen in many Tachinid flies (Refer Figure 4.24) where first-instar larvae actually escape from chorion during oviposition. Tachinid flies, are ovolarviparous, which means that embryos develop into first larval stage (instar) within eggs while still in female's oviduct. As a result, larvae hatch more rapidly or immediately after egg deposition (oviposition) and can begin feeding right away.

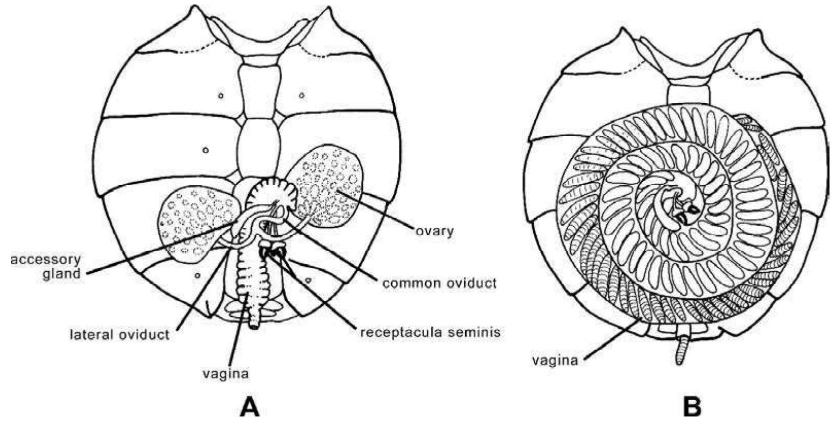

Fig. 4.24 *Female Reproductive System of Tachinid Fly*

The above Figure 4.24 shows the female reproductive system of tachinid fly, in which A. shows newly emerged fly; and B. shows mature female with very large vagina forming a brood chamber. An egg having a fully formed embryo is being laid.

3. Polyembryony

Polyembryony is the development of more than one embryos from one egg. Polyembryony is found in about 30 wasp species of parasitic Hymenoptera and one species of Strepsiptera. Availability to abundant nutrition along with transition from syncytial to total cleavage has resulted in development of this unique mode of reproduction. Thus, these insects are always associated with either parasitism or viviparity to get abundant of food.

General Life Cycle of Polyembryonic Wasps: All polyembryonic wasps (parasitic Hymenoptera) have similar life histories. They oviposit tiny and yolkless eggs into either life stages, such as egg or larva of host insect. Thus, chorion of egg is initially thin and permeable and becomes disappear rapidly. In parasitic wasps, serosa becomes modified for uptake of nutrients and is called as a trophamnion (Refer Figure 4.25). Each egg oviposited by a polyembryonic wasp grows into an individual embryo. Then an individual embryo produces additional identical embryos (or embryonic masses, Refer Figure 4.25) which collectively called as polymorula (or polygerm). Polygerm disintegrates and each embryo develops into a larva. The larvae feed within a host until all the usable parts are consumed and then pupate. At this stage, host insect is nothing more than a cuticular bag full of parasites. Number of broods formed by polyembryonic species of platygasterid and braconid wasps varies from two to hundred progenies. Some species of polyembryonic encyrtidae wasps give rise to thousands of progenies from a single egg.

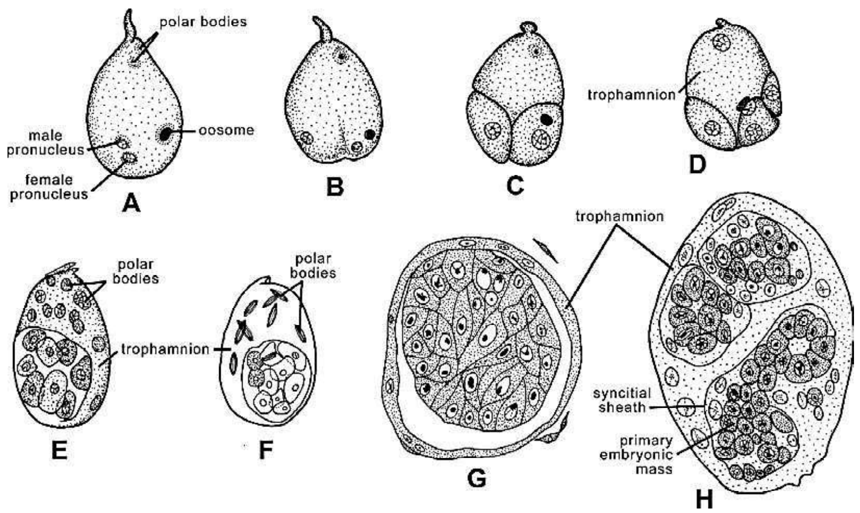

Fig. 4.25 *Early development of Parasitic Chalcidid Wasps*

The above Figure 4.25 represents the early development of parasitic chalcidid wasps, in which A. shows fertilization, B. shows first cleavage, C. shows two cell stage, D–F shows next stages; G. shows formation of spindle cells; and H. shows formation of secondary embryonic masses.

Polyembryony in Parasitic Encyrtidae Wasps

Events of Polyembryony are exclusively studied in the Encyrtidae wasp (*Copidosoma floridanum)*, that parasitises the Plusiine moths (*Trichoplusia ni)* (Refer Figure 4.26). Polyembryonic encyrtidae wasp has a caste system where different forms of larvae develop from the single egg. Different forms of larvae are morphologically and functionally are different. Parasitic wasp developed in host insect in following stages:

- **Cleavage Stage:** After laying egg, polar nucleus of Encyrtidae egg parts away rapidly from pronucleus. Eventually it moves to posterior pole of egg together with cytoplasmic pole plasm. Then initiation of first cleavage in Encyrtidae egg produces two equal-sized daughter cells (blastomeres) and an anterior polar cell having polar nucleus.
- **Polymorula Stage:** After host larva hatches, embryo of Encyrtidae wasp moves into proliferation phase of development. The primary morula undergoes division itself and produces 2–5 embryonic masses known as proliferative morulae that collectively form polymorula. All proliferative morulae have hundreds of round and non-differentiated cells enclosed by extra-embryonic membrane. Eventually all proliferative morulae subdivided through invagination of extra-embryonic membrane. It leads to production of more than 1000 proliferative morulae. These have around 40 cells each and by this time, host insect moults to fourth larval instar.
- **Soldier Larvae:** During this time, some secondary morulae undergo morphogenesis and develop to form soldier larvae. Soldier larvae are identified by their elongated body form and larger mandibles. Normally, about 4% of the total larvae produced from one host are soldiers form. These soldier larvae do not moult and die from desiccation when their reproductive caste siblings consume the host.
- **Reproductive Larvae:** At the same time, most of embryos undergo reproductive morphogenesis. At last days of host’s fourth instar and wasps develop to form a second caste known as reproductive larvae. When reproductive larvae are formed the host moults to fifth larval instar. These reproductive larvae are rounded body form and small mandibles.
- **Pupa and Adult:** Reproductive larvae rapidly consume insect host and then pupate which is enclosed as adult wasps. Whereas, soldier larvae become dead as reproductive larvae finish consuming the host.

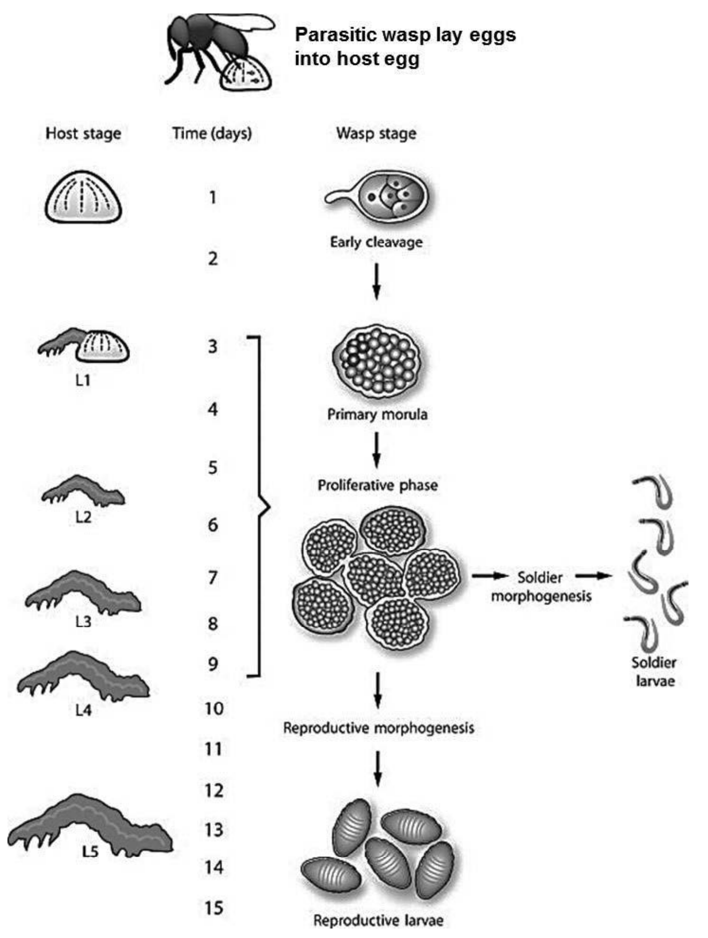

Fig. 4.26 Development of Polyembryonic Encyrtidae Wasp in its host Plussine Moths

4. Parthenogenesis

Eggs of some female insect species undergo development without fertilization of their eggs. This mode of asexual reproduction is called as **parthenogenesis**. Parthenogenesis is divided into two broad forms namely: Thelytoky and Arrhenotoky (Refer Figure 4.27).

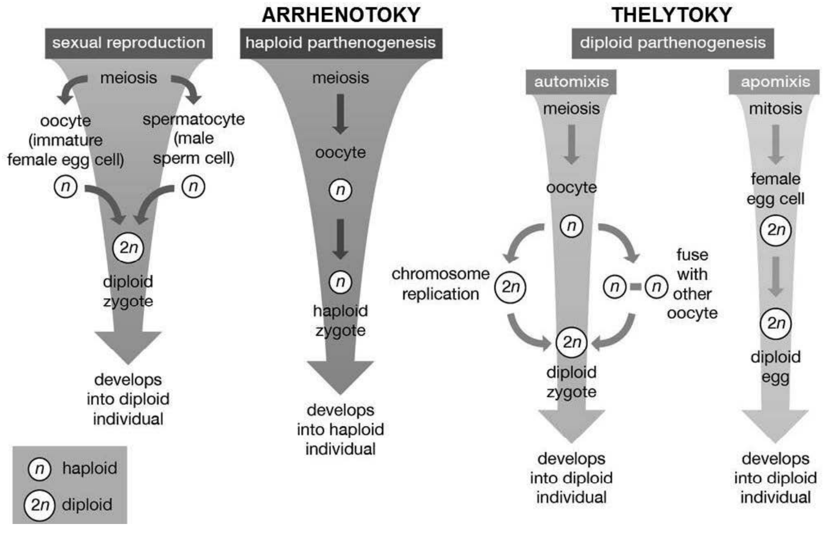

Fig. 4.27 Process of Sexual Reproduction Versus Different forms of Parthenogenesis in Insects

I. Thelytoky

In thelytoky, all unfertilized eggs develop to form diploid females. This is also called diploid parthenogenesis. Thelytoky is found in insects, such as Bugs, Thrips, Stick insects and Booklice. Two forms of female-producing parthenogenesis (thelytoky) are discussed below:

- **Ameiotic or Apomictic Parthenogenesis:** In some species no meiotic division occurs during oogenesis. This mode of thelytoky parthenogenesis is called as ameiotic or apomictic parthenogenesis. This type of parthenogenesis involves a process of apomixis. Therefore, offspring are diploid and female. Offspring will have the same genetic makeup as the mother. Genetic makeup can change if mutation or insertion of transposable elements occurs. Examples are aphids, weevils and long-horned grasshoppers.
- **Meiotic or Automictic Parthenogenesis:** In this type parthenogenesis, automixis occurs where meiotic division takes place and diploidy of egg is restored without fertilization. Thus, typical reduction division is followed by nuclear fusion so that a diploid chromosome is retained. Therefore, offspring are diploid female but they have a different genetic makeup from their mother. Examples are some bugs, wasps and butterflies.

Thelytokous Parthenogenesis (Apomictic) in Aphids

Aphids reproduce for most of year by ameiotic or apomictic parthenogenesis (Thelytoky) (Refer Figure 4.28). Aphids alternate parthenogenetic generations in spring and summer with a normal sexual generation in autumn. In following steps aphids maintains their population in unfavourable season and increase their genotype in favourable season:

- When autumn season comes, asexual females produce sexual male and female. During maturation of some oocytes, a separation of two X chromosomes occurs. One of these migrates to polar body and is destroyed. From such eggs with an X0 chromosome, males will develop. As spermatogenesis occurs in these individuals, spermatocytes containing either one or no X chromosome are produced. Spermatocytes with no X chromosome (A0) do not mature, so that only sperm with an X chromosome (AX) produced. Therefore, overwintering eggs produced as a result of mating will have an XX sex chromosome and diploid for both types of chromosomes (AA: Autosome and XX: Sex).
- When winter comes, eggs remain in diapause and thus called as overwintering eggs.
- When spring comes, these overwintering eggs (AAXX) give rise only to asexual and diploid females.
- During spring and summer, asexual females undergoes many cycles of apomictic parthenogenesis.

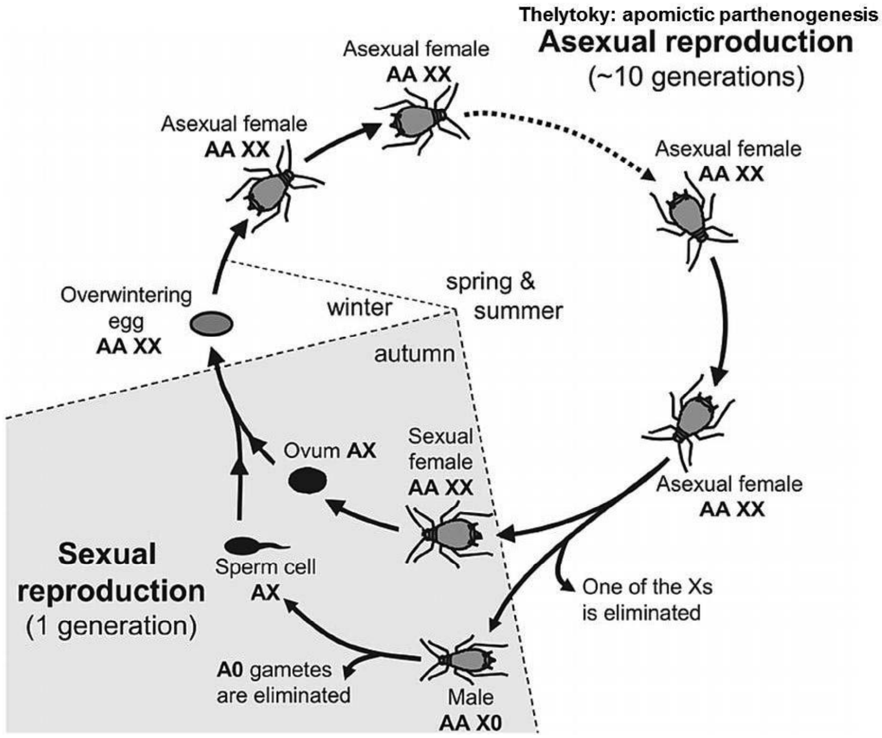

Fig. 4.28 *Annual Life-Cycle of Pea Aphid Alternate with Apomictic Parthenogenesis and Sexual Reproduction*

II. Arrhenotoky

In arrhenotoky, unfertilized haploid eggs grow into males and fertilized diploid eggs grow into females. Arrhenotoky also called haplodiploidy is usually occurring in wasps and bees (Hymenoptera) and thrips (Thysanoptera). Arrhenotoky also found in whiteflies and scale (Hemiptera) and some beetles. In haploid parthenogenesis (arrhenotoky), oocyte nucleus undergoes meiosis that is not followed by nuclear fusion. This is relatively rare in occurrence and results in production of males.

Arrhenotoky in Bees and Wasps

Bees, ants and wasps (Hymenoptera) show haploid parthenogenesis (arrhenotoky). Female insects decide whether or not to fertilize her egg by controlling release of sperm from spermatheca as eggs move down oviduct. In this way, mother regulates sex ratio of her progeny.

Therefore, in Hymenoptera, haploid parthenogenesis is facultative that is a female determines whether or not an egg will be fertilized. In honey bee, a queen normally lays fertilized eggs that develop into workers (diploid females). But, under some conditions, for example, when hive is crowded and workers construct larger than normal drone cells on honeycomb. Then she will lay unfertilized eggs from which haploid males develop (Refer Figure 4.29.).

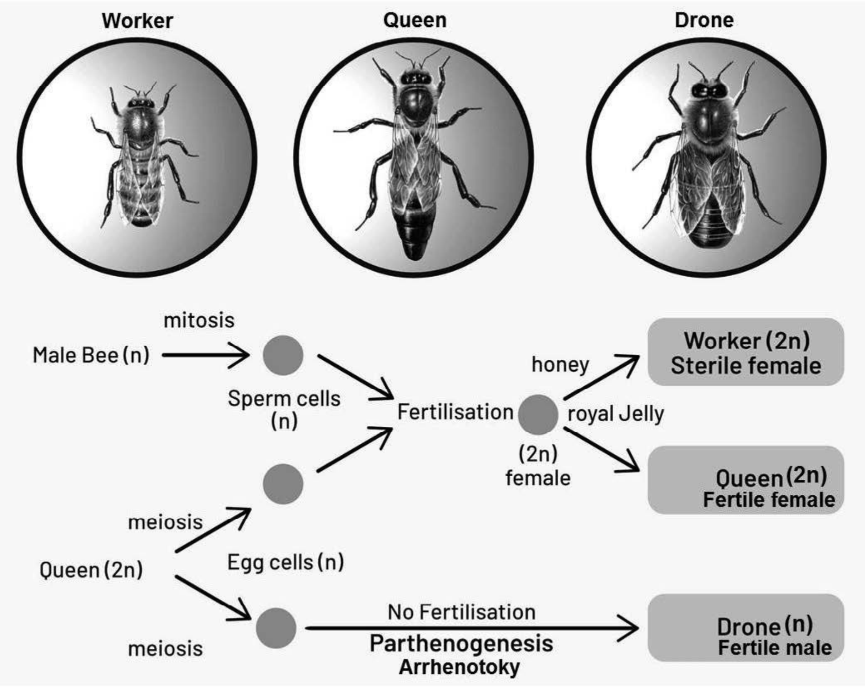

Fig. 4.29 *Arrhenotokous (Haploid) parthenogenesis in Honey Bees*

Advantages of Parthenogenesis

- In an insect whose population density can be temporarily low, the ability of an isolated female to reproduce parthenogenetically. It ensure survival of her genotype until population density increases and males are again likely to be encountered. Thus parthenogenesis avoids sterility in races.
- A parthenogenetic female does not require to locate or be located by a male for mating. She can utilise her time and energy to egg production and feeding. All her offspring are female, so that her maximum reproductive potential can be maximized.
- Parthenogenesis serves as the means for the determination of sex in honey bees, wasps, etc. It is the best way of high rate of multiplication in certain insects, for example aphids.
- Parthenogenesis encourages development of advantageous mutant characters. It also checks the non-adaptive combination of genes which can be caused due to mutation.

Disadvantages of Parthenogenesis

- Individuals produced due to parthenogenesis are not much successful in struggle for existence. Due to the fact that no recombination of genetic material occurs hence, variations are not produced.
- Genotype of successive generations remains more or less constant so that adaptation of a species to changing environmental conditions is very slow. To counteract this, many species alternate one or more parthenogenetic generations with a normal sexual generation.

NOTES

5. Pedogenesis

Several insects mature sexually rapidly in early life stage and thus are able to reproduce in larvae or pupae stage. This mode of reproduction is called as pedogenesis. Most of insects with pedogenesis are also viviparous and parthenogenetic in reproduction. In gall midges and wood midges (Cecidomyiidae), larvae reproduce larvae or sometimes oviposit eggs. Pupal forms of some gall midges (*Tekomyia and Henria)* produce larvae.

Pedogenesis in Telephone-Pole Beetle

Telephone-pole beetle (*Micromalthus debilis*) consists of five reproductive forms, such as male-producing larvae, female-producing larvae, adult males, adult females and larvae producing males and females (Refer Figure 4.30). This insect species involves complex heteromorphosis. Life-cycle of Telephone-pole beetle is explained as follows:

- Two different types of parthenogenesis are thelytoky, arrhenotoky. Both of these occur in paedogenetic larva of this insect.
- In arrhenotoky and oviparity form, the larva lays one egg, which then gives rise to a larva that eat mother and develops into a male beetle.
- In arrhenotoky and viviparity form, paedogenetic larva gives birth to about ten small larvae of triungulin type. First instar *larva* in beetle has three claws on each foot and is therefore called as *triungulin.* These are very active and can disperse easily in decaying wood. Triungulin larva passes through a number of moults to become cerambycoid larva, which develops into female beetle.
- But more commonly, this cerambycoid larva moults into a paedogenetic larva and the cycle of larval reproduction starts again.
- Larva grows over several instars before undergoing complete metamorphosis to become an adult. Individual female and male can reproduce sexually by undergoing complete metamorphosis instead of parthenogenesis.

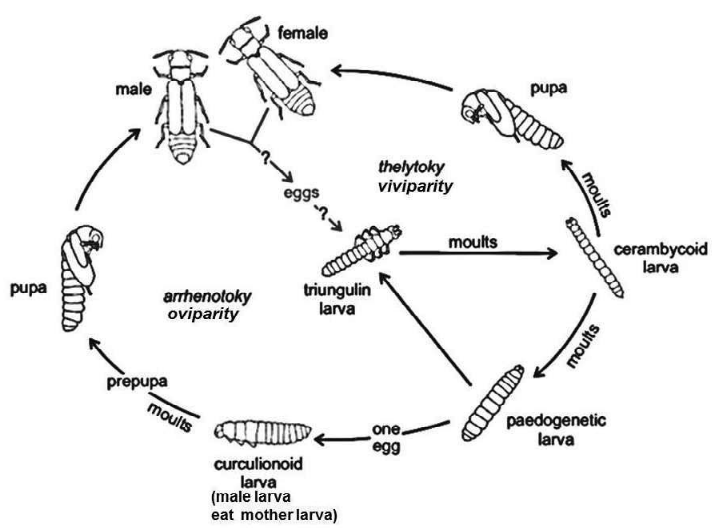

Fig. 4.30 Life Cycle of Telephone-Pole Beetle (Micromalthus debilis)

Check Your Progress

17. What are oviparous insects?
18. What is viviparity?
19. Where does female insects keep their eggs in ovoviviparity?
20. Define the term polyembryony.
21. What is parthenogenesis?
22. What is pedogenesis?

4.5 FERTILIZATION AND EMBRYONIC DEVELOPMENT

After mating and sperm transfer in insects, fertilization of ova takes place in female insects that eventually initiates embryonic development in fertilized egg called zygote. Fertilization and embryonic development is discussed in detail under following sections:

- Events Before Fertilization: Ovulation, monospermy, polyspermy and sperm utilization.
- Events During Fertilization: Sperm capacitation, sperm entry to egg, sperm penetration, egg activation and amphimixis.
- Events After Fertilization: Oviposition, embryonic development and egg hatch.

4.5.1 Events Before Fertilization

After sperm transfer, ovulation and sperm utilization occur in female reproductive organ. Monospermy and polyspermy are also the aspects that vary in insects before an egg or ova get fertilized.

1. Ovulation

An egg gets fertilized when it moves into common oviduct and genital cavity where a few sperm are released from the spermatheca. This event of egg release is called as ovulation. Ovulation is the movement of an egg from the ovary into the lateral oviduct. This also provides stimulus to maturation of oocytes (Refer Figure 4.31).

In some insects, egg can or cannot be well separated in time from the actual process of egg laying (oviposition). In most insects, those lay their eggs singly (for example assassin bugs), oviposition immediately follows ovulation. In insects that deposit eggs in batches or are viviparous, the two events occur several days apart. For example, in Locusts, eggs accumulate in lateral oviducts for a week before being fertilized and laid.

2. Monospermy and Polyspermy

Several spermatozoa enter egg. Only one of these is usually utilized in fertilization of egg. This called as monospermy. Polyspermy is the entry of two or more sperm into an egg and is common in insects. But only one sperm normally undergoes transformation into a pronucleus and the rest of sperm degenerate. In fruit flies, some eggs are monospermic and many eggs receive 30 or more spermatozoa and thus are polyspermy. But in some insects, several female nuclei are found. For example, butterflies and moths have binucleate eggs and thus each is fertilized by a different spermatozoon.

3. Sperm Utilization

Utilization of sperm can well be a very efficient process. For example, founding queens of leafcutter ants use only two sperm for single egg for fertilization, whereas older queens use three sperm for single fertilized egg. In this manner queens retain their fertility for up to ten years or more even they do not further mate.

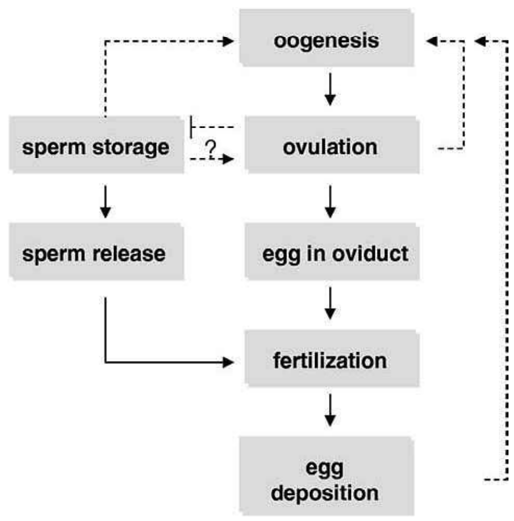

Fig. 4.31 Sequence of Events (Solid Line) and their Possible Effects (Dashed Line) for Egg Development and Fertilization

4.5.2 Events During Fertilization

Insects have internal fertilization that is eggs are fertilized inside female body. Fertilization is the penetration of a mature ovum by spermatozoon and fusion of respective male and female pronuclei. It results in zygote formation that is fertilized egg. The process of fertilization can take place in following steps:

1. Sperm Capacitation

In many insects, sperm undergo modifications when transferred to female spermatheca. These modifications are crucial before sperm can fertilize ova. This event of sperm maturation within female body is called as sperm capacitation.

- In Housefly, sperm eliminate plasma membrane from head and most of granular material from acrosome.
- In butterflies and moths, dissociation of eupyrene sperm bundles in spermatophore is assisted by activation of apyrene sperm. A specific protease from lower simplex is responsible digestion of glycoprotein covering flagellar membrane of apyrene sperm. The same protease releases arginine from proteins in seminal fluid. Arginine is metabolized to 2-oxoglutarate, a substrate

for sperm activity. Also cyclic AMP (Adenosine Monophosphate) is important for activation of sperm.

2. Sperm Entry to Egg

In almost all insects sperm enter eggs as the egg pass through common oviduct during oviposition. The entry of sperm involves two events; i. release of sperm from spermatheca in synchrony with movement of an egg through oviduct; and ii. sperm locate the micropyle of egg. Sperm move into the egg through one or more micropyles that are narrow canals across through eggshell. Micropyle is located towards opening of spermatheca duct at time of egg passage, enabling entry of sperm. Usually several sperm penetrate each oocyte and fertilization takes place by only one of the sperm whereas remaining sperm degenerate.

Micropyles also vary in number with insect species. For example, eggs of many flies have only one terminal micropyle whereas grasshoppers have 30-40 micropyles arranged in a ring shape at posterior end of egg. But spermatozoa enter one of the micropyles. Sperm motility is increased when sperm approach micropyle.

3. Sperm Penetration

Mechanisms associated with sperm penetration into egg are not well studied. In small fruit flies (*Drosophila*) sperm cell penetrates the egg with its plasma membrane, which covers nucleus and whole flagellum. But sperm-egg membrane fusion does not occur. Thus, passage of male gamete through micropyle does not involve an acrosomal reaction. *Drosophila* spermatozoa have an acrosome at tip of nucleus but this membrane-bound structure penetrates egg at fertilization where it remains detectable throughout zygote formation.

4. Ovum Activation

As spermatozoon accesses the egg nucleus and shedding its tail, subsequently it transformed into male pronucleus. Then the two maturation divisions of the female egg occur rapidly upon one another. Completion of two meiotic divisions of oocyte nucleus gives rise to three polar body nuclei and the female pronucleus. Polar body nuclei normally migrate to periphery of oocyte (Refer Figure 4.32A) and eventually degenerate.

5. Amphimixis

During fertilization, penetration of a spermatozoon into ovum initiates ovum activation and amphimixis. Amphimixis is the union of male and female gametes. Ovum activation results in formation of female and male pronucleus and also three polar nucleus bodies. These polar bodies degenerate during amphimixis but in parasitic wasps two polar bodies fuse to form polar nucleus. Subsequently, amphimixis results in fusion of male and female pronuclei that produces diploid (2n) zygote. In parasitic wasps, fused nucleus lies in posterior region of egg, whereas polar nucleus made by fusion of two polar bodies lies in anterior (Refer Figure 4.32B-D).

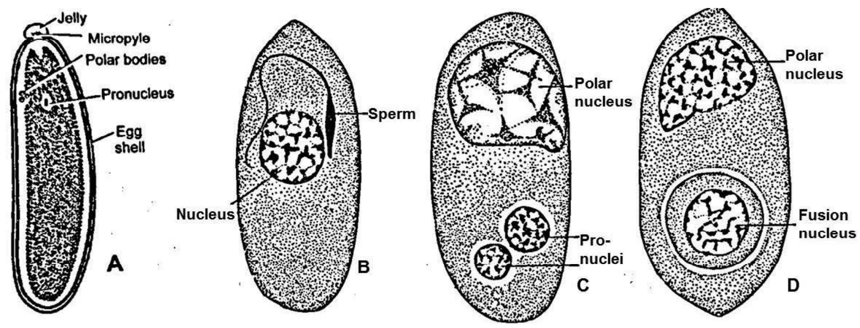

Fig. 4.32 *A. Egg Activation in Housefly (Musca), and (B-D) Amphimixis in Parasite Wasps (Platygaster), B. Egg (with Sperm) One Hour after Oviposition, C. Male and Female Pronuclei about to Fuse; and D. Egg with Fused Pronucleus One to Two Days Old*

Sex Determination in Insects

The sex of an insect is almost always determined genetically. Most insects are diploid that is having one set of chromosomes from each parent. Most bisexual organisms produce 1:1 sex ratio. This is achieved by having one heterogametic sex and other homogametic sex. Followings are basic three different systems of sex determination occur in different insects:

i. **XX/XY System:** The XX/XY sex-determination system occur in some insects. For example, in small fruit fly (*Drosophila*), female is homogametic sex and contains XX chromosomes; and male is heterogametic sex and contain XY chromosomes. The X and Y sex chromosomes are different in shape and size from each other (Refer Figure 4.33).

XX × XY (parents) → 1:1 XX and XY (progeny)

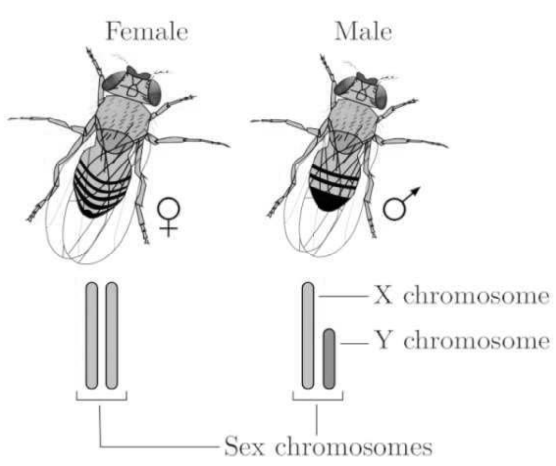

Fig. 4.33 *Sex Chromosomes in Small Fruit Fly (Drosophila)*

ii. **XX/XO System:** Sex of progeny corresponds to presence of one, i.e., XO or two, i.e., XX, sex chromosomes. XX is usually female and XO is usually male. The zero (the letter O or 0) denotes lack of a second X chromosome. XX/XO sex determination occurs in crickets, locusts and grasshoppers (orthopteroid insects), many bugs and beetles.

NOTES

XX (female parent) × XO (male parent) → 1:1 XX and XO progeny

iii. **ZW/ZZ System:** Butterflies and moths (Lepidoptera) have a different sex-determination system. In this female is the heterogametic sex. The sex chromosomes are denoted as Z and W. This system of sex determination is called as ZW/ZZ. Thus females contain ZW chromosomes and males contain ZZ chromosomes.

ZW (female parent) × ZZ (male parent) → 1:1 ZZ and ZW (progeny)

4.5.3 Events After Fertilization

After fertilization of eggs in female body, fertilized egg deposited, and then embryonic development begins with first mitotic division of zygote nucleus and terminates at hatching.

1. Oviposition

After fertilization of eggs in female body, eggs are deposited outside environment by oviparous insects. This process is called **oviposition**. The readiness to oviposit occurs upon mating. A female silk moth, lays all her eggs within 24 hours of mating. It is induced by peptides or other substances transferred to female by male during sperm transfer. These substances cause female to seek an oviposition site. When she receives stimulation from her mechanoreceptors and chemoreceptors, begin ovipositing.

Females of many insects attach their eggs, either singly or in batches to surface (food source) using secretions of accessory glands. Such insects usually lack an ovipositor. Gonopore of female insect is usually situated on or behind eighth or ninth abdominal segment act as ovipositor. Other insects lay their eggs in crevices or in plant or animal tissues, using an ovipositor. In butterflies, beetles and flies, terminal segments of abdomen are long and telescopic that form ovipositor.

2. Embryonic Development

Embryonic development of fertilized egg is called as embryogenesis. When egg pronucleus and sperm fuse results in fertilization and formation of a diploid zygote. At this point, embryogenesis proceeds through a series of steps or processes namely cleavage, blastoderm and germ band formation, gastrulation, segmentation and organogenesis (Refer Figure 4.34). Then embryonic development ends with egg hatch. Thus it involves multiplication of cells (by mitosis) and their subsequent growth, movement and differentiation into all tissues and organs of an insect.

Fig. 4.34 *Sequence of Events during Embryonic Development in Insect Egg*

i. Cleavage

Cleavage is developmental process after fertilization. Zygote nucleus begins to divide mitotically and undergoes a number of mitotic divisions. Insects have syncytial cleavage that is they have only nuclear divisions. Thus, each nucleus in early embryo of insect is enclosed by a halo of cytoplasm developed during syncytial cleavage and is known as an **energid** (Refer Figure 4.35A).

For example, zygote of fruit flies (*Drosophila*) undergoes around 13 numbers of mitotic divisions during cleavage. During seventh nuclear division majority of energids start moving to periplasm of egg (Refer Figure 4.35B). In this by time of cycle ten they dispense themselves as a monolayer at surface of egg. This monolayer is known as **syncytial blastoderm** (Refer Figure 4.35 C and E).

Total or Complete Cleavage: In many animals, early cleavage is division of both cytoplasmic and nuclear material to form cells known as blastomeres. This type of cleavage is called as total or complete cleavage. In this, mitosis results in formation of true cells and each is enclosed by a plasma membrane. But most of insects do not have total cleavage. Total cleavage occurs in small eggs of some endoparasitic wasps and springtails.

Syncytial Cleavage: Cleavage in insects consists of only nuclear division (karyokinesis) without undergoing division of cytoplasm (cytokinesis) or formation of a plasma membrane. This type of cleavage is called as syncytial cleavage.

ii. Blastoderm and Vitellophages Formation

After arrival at periplasm, energids continue to divide, until the nuclei become closely packed. This is the syncytial blastoderm stage (Refer Fig. 4.35 C and E). After this, cell membranes form by radial infolding, then tangential expansion of original egg plasma membrane. This is uniform blastoderm stage (Refer Figure 4.35 D and F). In *Drosophila*, the plasma membrane infolded between nearby nuclei in the periplasm during the fourteenth cycle of mitosis. Layer of cells produced at periphery of egg is a cellular blastoderm.

Most of energids move to surface of egg to form the blastoderm. But some energids remains in yolk to form yolk cells that is called as **vitellophages**. Vitellophages have different functions along with breakdown and engulfment of yolk into vacuoles. When yolk is surrounded in midgut, vitellophages form part of midgut epithelium.

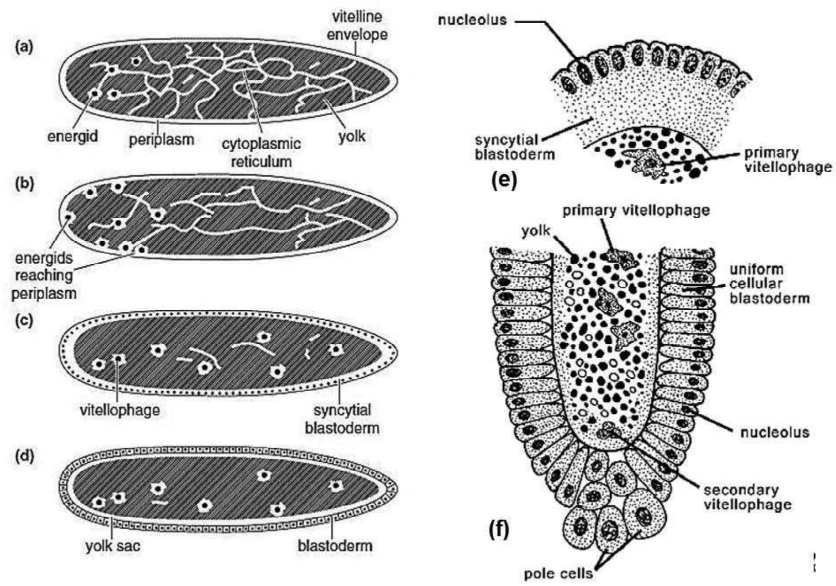

Fig. 4.35 *Syncytial Cleavage and Early Development in Egg Leading up to Formation of Blastoderm in a Fly. E. and F. are enlarged view of C. and D. Respectively*

iii. Formation of Germ Band

In most insects, blastoderm is a single and uniform sheet of cells which covers surface of egg and encloses yolk. After this, an area of blastoderm thickens to form more columnar cells. These are called as **germ anlage** and then it developed to form germ band (Refer Figure 4.36 and 4.37).

Size and position of germ anlage (embryonic primordium) vary with insects (Refer Figure 4.36 and 4.37). In insects, for example fruit flies, honey bee, silk moths, lacewings, germ anlage develops from nearly entire blastoderm are referred to as long-germ-type embryos.

In most insects, anterior region is expanded laterally as a pair of head lobes called as protocephalon (Refer Figure 4.37 and 4.38). Behind which is a region of varied length, the protocorm (postantennal region).

Blastoderm cells that do not participate in formation of germ band differentiate into an extra-embryonic membrane called as serosa. A second membrane called as amnion develops shortly after formation of serosa from cells adjacent to germ band (Refer Figure 4.37 and 4.38).

Growth of germ band occur either on surface of yolk (superficial growth) (Refer Figure 4.37) or by immersion into yolk) (Refer Figure 4.38). Immersion of germ band called as **anatrepsis**. It forms first of a series of embryonic movements, collectively known as **blastokinesis**. Reverse movement is called **katatrepsis** (Refer Figure 4.38), which brings embryo back to surface of yolk, occurs later.

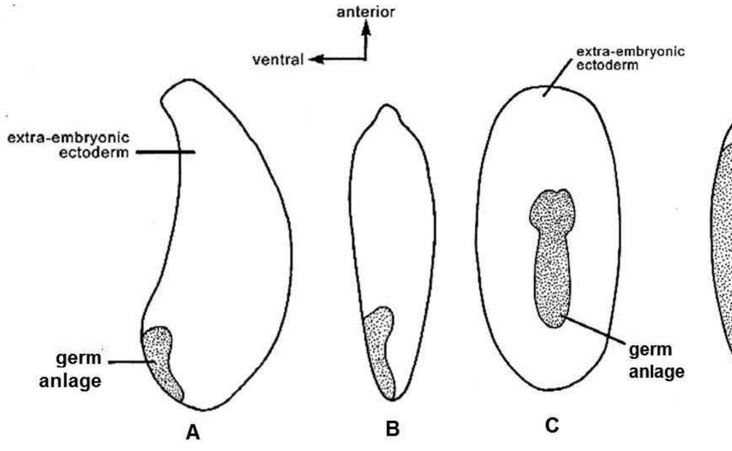

Fig. 4.36 *Size and Position of Germ Anlage (Shaded) in Eggs of Different Insects, Exopterygotes: A. Cockroach, B. Damselfly; Endopterygotes: C. Darkling Beetles; and D. Alderfly*

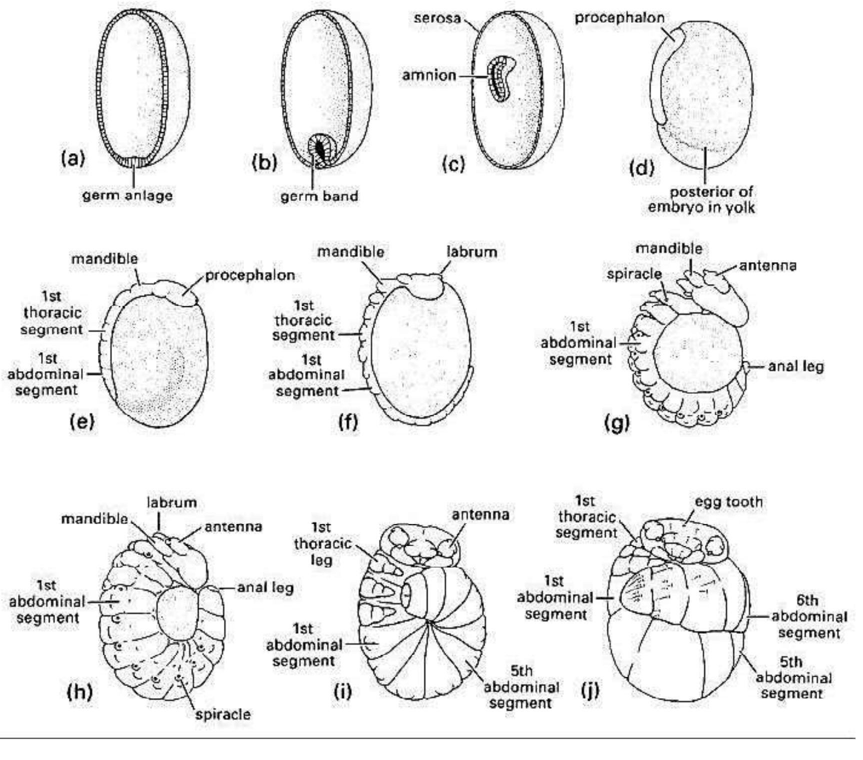

Fig. 4.37 *Embryonic Development in Scorpionfly, Age of Insect Egg Counted from Oviposition: A. 32 Hours, B. 2 Days, C. 7 Days, D. 12 Days, E. 16 Days, F. 19 Days, G. 23 Days, H. 25 Days, I. 25–26 Days; and J. Completely Developed at 32 Days*

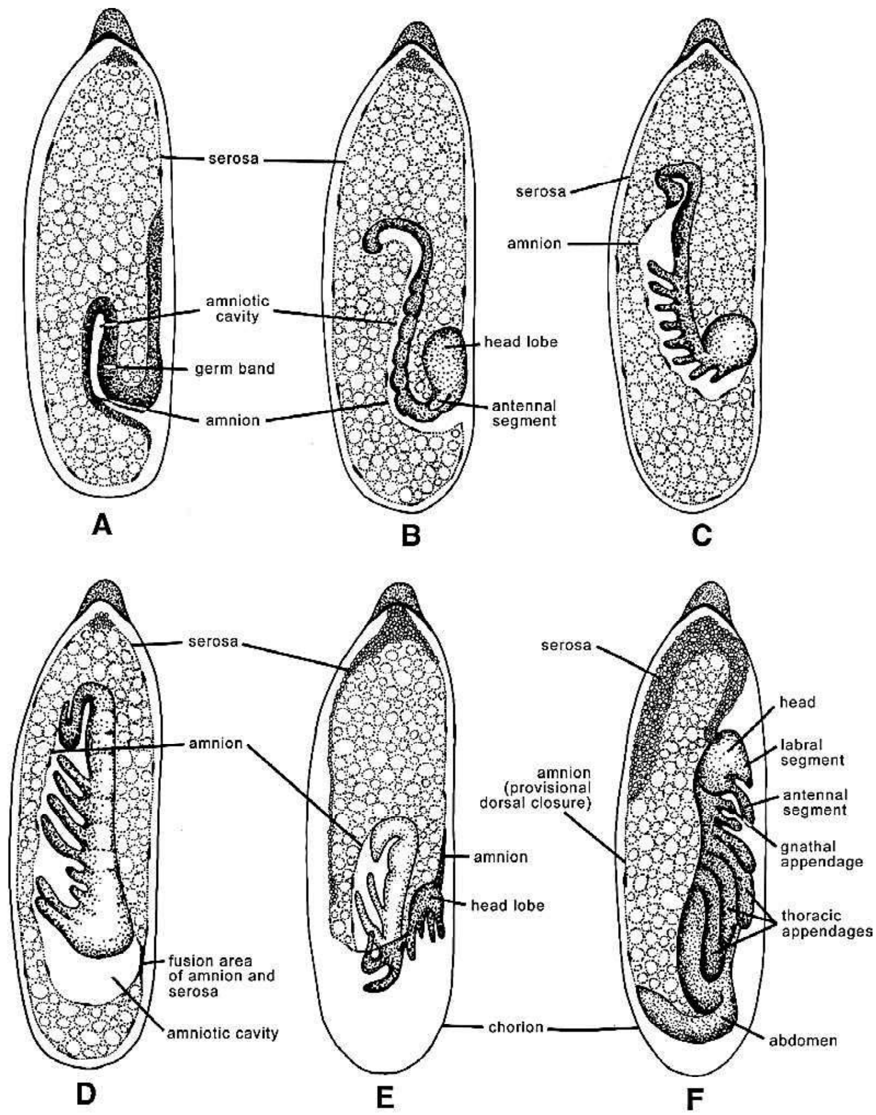

Fig 4.38 *Early Embryonic Development in Large Damselfly to Show Anatrepsis and Katatrepsis*

iv. Gastrulation

Gastrulation is process of invagination and proliferation of cells along midline in egg. During gastrulation, single-layered germ anlage develops into two-layered germ band. Germ band elongates and becomes broader. Thus, segmentation and limb-bud formation in embryo appear externally (Refer Figure 4.40D). These are followed by germinal layers and somite formation. Followings are detailed events take place during gastrulation:

- **Gastral Groove:** As germ band begins to increase in length and its mid-ventral cells sink inward to form a transient, longitudinal gastral groove (Refer Figure 4.39A). Invaginated cells soon separate from outer layer, which closes to eliminate groove. It is from anterior and posterior points of closure of gastral groove that stomodeum (foregut) and proctodeum (hindgut), respectively, develop.

- **Formation of Germinal Layers:** Outer layer of embryo is embryonic ectoderm. In majority of insects, most outer cells in contact with amniotic cavity form ectoderm. Generally, cells near the yolk form mesoderm. Thus, invaginated cells, which proliferate and spread laterally, form mesoderm (Refer Figure 4.39B) except adjacent to developing foregut and hindgut where they become anterior and posterior midgut rudiments, respectively. The anterior and posterior midgut rudiments are third germinal layer called endoderm. Mesodermal cells become concentrated into paired longitudinal tracts which soon separate into segmental blocks, leaving only a thin longitudinal strip, median mesoderm, from which haemocytes differentiate. From these segmental blocks, paired hollow somites usually arise (Refer Figure 4.39B).
- **Somite Formation:** Somite formation is initiated and occurs simultaneously in gnathal (mandibular, maxillary, and labial) and thoracic segments, spreading anteriorly and posteriorly after gastrulation takes place (Refer Figure 4.39B). Formation of coelom (cavity within a somite) occurs in one of two ways, by internal splitting of a somite or by median folding of lateral part of each somite.
- **Formation of Amnion and Serosa:** Two extra-embryonic membranes called amnion and serosa, develop from extra-embryonic ectoderm (Refer Figure 4.37C and 4.39B, C). Cells at edge of germ band proliferate and tissue formed on each side folds ventrally to give rise to amniotic folds. These meet and fuse in ventral midline to form inner and outer membranes called as amnion and serosa, respectively. Amnion encloses a central fluid-filled amniotic cavity.
- **Katatrepsis:** Germ band forms ventral regions of future body, which progressively differentiates with head, body segments and appendages becoming increasingly well defined (Refer Figure 4.37E-G). At this time, embryo undergoes movement called katatrepsis, which brings it into its final position in egg.
- **Dorsal Closure:** Near the end of embryogenesis (Refer Figure 4.37H, I), edges of germ band grow over remaining yolk and fuse mid-dorsally to form lateral and dorsal parts of insect. This process is called as **dorsal closure**. In embryos of most insects, amnion and serosa fuse in vicinity of head and combined tissue then splits to expose head and rolls back dorsally over yolk (Refer Figure 4.39C). As a result, serosa is reduced to a small mass of cells, secondary dorsal organ and amnion becomes stretched over yolk, forming provisional dorsal closure (Refer Figure 4.39D). Then definitive dorsal closure occurs which is enclosing of yolk within embryo. It occurs by a lateral growth of embryonic ectoderm, which gradually replaces amnion or rarely serosa (Refer Figure 4.39D).

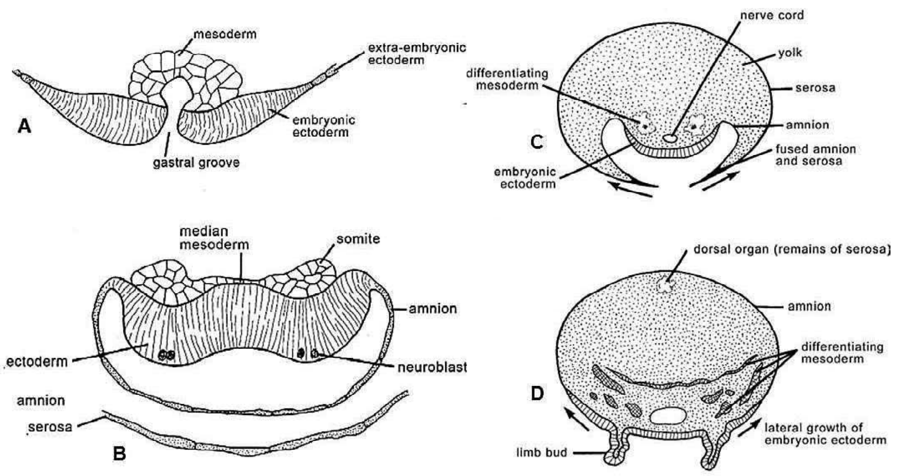

Fig. 4.39 *Gastrulation in Locusts, A-B. Formation of Gastral Groove, Somites, and Embryonic Membranes; Dorsal Closure: C. Initial Fusion of Amnion and Serosa and Beginning of Rolling Back; D. Provisional Dorsal Closure with Amnion Covering Yolk*

V. Organogenesis

During gastrulation, germ band elongation and segmentation are complete, limb buds develop the embryonic layers grow and internally organogenesis begins. As a result of gastrulation, three primary germ layers or embryonic layers become distinctly organized. These are endoderm, ectoderm and mesoderm. The development of various organs from these three germinal (or germ) layers is called as organogenesis.

i. Ectoderm

- **Epidermis and Appendages:** Most of cells developing into outside wall are epidermal cells which together develop into epidermis. Epidermis in embryos of most insects then secretes first instar larval cuticle. Each of appendages in immature insect develops through outgrowth of body wall. Labrum forms in opposite of foregut and antennal rudiments develop on either side of protocephalon. Origins of mandibles, maxillae and labium (gnathal segments) are situated behind protocephalon (or head lobe).
- **Nervous System**: Central Nervous System (CNS) develops from cells of neurogenic ectoderm on ventral side of the embryo. Individual cells divide peripherally; dividing large cells and then develops into neuronal stem cells referred as neuroblasts.
- **Trachea System:** Respiratory system or trachea forms from each segment. Each metameric unit initiates its development autonomously at the time of germ band formation where sets of tracheal cells distinguish and are retain aside from adjacent epidermal cells.
- **Gut and Malpighian Tubules:** Portions of gut and Malpighian tubules formed ectoderm. Foregut and hindgut are formed from stomodeum and proctodeum, respectively. Malpighian tubules arise as outgrowth from tip of proctodeum.

- **Other Organs:** A number of ectodermal invaginations develop, from which differentiate endoskeletal components, various glands and some parts of reproductive tract. Salivary glands develop from a pair of invaginations near bases of labial appendages.

ii. Mesoderm

- **Body Cavity:** In some insects, such as ants, coelomic cavities form as clefts in somites. In other insects, such as Locusts, mesoderm rolled up to enclose a cavity.
- **Muscles and Fat Body:** Many tissues, such as muscles and fat body (that are the primary metabolic organ of insects) develop from mesoderm. Somatic muscles are developed from cells called as myoblasts.
- **Circulatory System:** Dorsal vessel of insect is developed from cells known as cardioblasts, arising from upper slant of coelomic sacs. Aorta is formed by median walls of antennal coelomic sacs on either side. Median mesoderm gives rise to haemocytes.
- **Reproductive System:** Reproductive system develops from both mesoderm and ectoderm,
  - In female exopterygotes, vagina and spermatheca develop after hatching as mid-ventral ectodermal invaginations of seventh or eighth abdominal segment. In males, ejaculatory duct and ectodermal accessory glands are formed from mid-ventral invagination of ectoderm of ninth or tenth abdominal segment.
  - Mesoderm that forms gonads originates from numerous segments. The rudiment thickens on ventral and produces compact strands of cells in which cavities results to develop into lateral ducts. Median ducts develop from infoldings (invaginations) of ectoderm.

iii. Endoderm

Midgut: Invaginations of stomodeum and proctodeum contain anterior and posterior origins of endoderm. They expand toward each other to form paired longitudinal strands of tissue underneath yolk and above visceral mesoderm. Midgut tissue from these strands expands over surface of yolk, ultimately surrounding it and developing complete gut.

3. Egg Hatch

After completion of embryonic development, hatching of eggs occurs. Egg hatch is escape of neonate larvae or nymphs from embryonic membranes. Mechanisms of egg hatch vary with different insects. For example, caterpillars in butterflies and moths chew embryonic membranes and chorion to make their way. Neonates of other insects rupture chorion by body movements. In dragonflies, pulsating organ or cephalic heart creates pressure against egg shell and pushes up a cap like operculum. Thus it provides exit of insect.

Fertilization and Embryonic Development in Different Insects

1. Cockroach

Ootheca Formation and Fertilization: Mature eggs are elongate oval in shape. Sixteen eggs one from each ovariole descends together through vulva into vestibulum of genital pouch. When they are laid become fertilized by sperms ejected simultaneously from spermatheca. Sperm enters through micropyle of egg shell. Fertilized eggs surrounded by secretion of collaterial glands, which hardens to form an egg case or ootheca. Sixteen eggs are arranged in two rows in one ootheca, assisted by ovipositor valves. Complete formation of ootheca occurs within two days. It protrudes behind her abdomen. A total of about 15 ootheca are oviposited by female cockroach.

Laying of Ootheca: Female cockroach carries ootheca for several days, till it is deposited in a warm, sheltered and dark place.

Embryonic Development: Fertilized eggs are slightly curved, concave on one side and convex on other side. Each has diploid nucleus and sufficient yolk, supplying enough food for embryonic development. Each egg undergoes superficial characteristic of insects, resulting in blastula followed by gastrulation. Gastrula is differentiated into embryo which gets separated from blastoderm by an amniotic cavity. Its three germ layers namely ectoderm, mesoderm and endoderm form various parts of nymph.

Hatching: When hatching occurs, dorsal keel of ootheca splits and nymphs emerge out leaving their egg membranes behind. Freshly hatched nymphs are delicate, transparent and colourless in appearance. They resemble almost adults but differ in size and colouration, in being sexually immature and lacking wings.

2. Honey Bee

Fertilization: Liberation of spermatozoids is dependent on opening of muscular sphincter of spermatheca. With these muscles, queen is able to control aperture of spermathecal duct. Thus, she is able to release small doses of sperm. Within vagina there is a valve fold which the queen is able to press unfertilised egg up towards the entrance to the spermathecal duct. The release sperm will enter the egg via the micropyle. Thus, queen may or may not fertilize eggs before laying:

- Fertilized eggs give rise to females (diploid individuals with 32 chromosomes).
- Unfertilised eggs give rise only to males, which are haploid (n = 16), which means the multiplication of sexual cells without meiosis. It is the phenomenon of parthenogenesis arrhenotoky.

Oviposition: Egg laying can start about 2 days after mating and proceeds regularly and continuously, except during periods of cold weather. Fertilized eggs are deposited in cells of workers or queens and non-fertilized ones in drone cells.

Embryonic Development: In honey bee, germ anlage develops from nearly entire surface of blastoderm and thus known as long-germ-type embryos (Refer Figure 4.40). This results in germ anlage giving rise to complete body plan (head, thoracic and abdominal segments) of future insect, with all body segments forming nearly simultaneously once formation of germ band is complete. Germ band of long-germ-type embryo extends very little.

Egg Hatching: These are whitish and elongated. At deposition they are vertical on cell bottom, attached by one end, then oblique and finally become horizontal on third day. Duration of egg incubation is three days.

NOTES

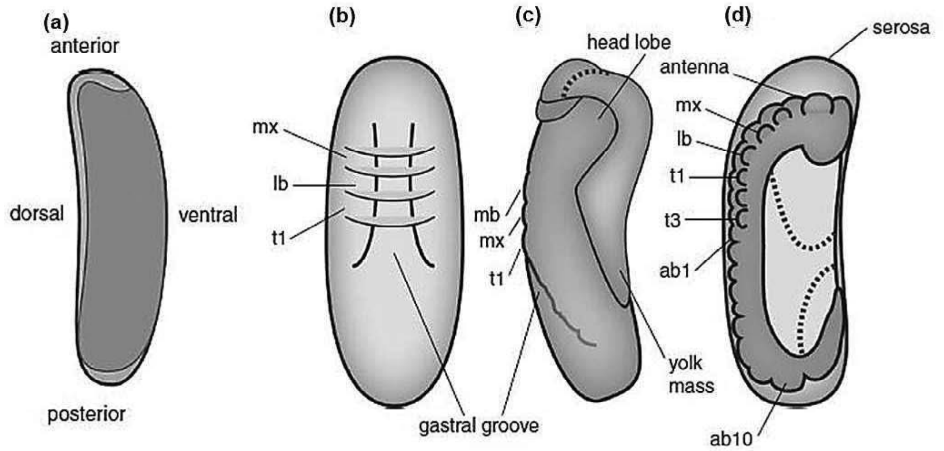

***Fig. 4.40** Elongation and Segmentation of Germ Band in Honey Bee*

In above Figure 4.40 Elongation and segmentation of germ band in honey bee is shown, in which A. shows the size and position of germ anlage (shaded) in egg, B. shows ventral view at early gastrulation, C. shows lateral view at the end of gastrulation; and D. shows lateral view after completion of segmentation. The abbreviations used in the figure are as follows; Mb: Mandibular segment; mx: Maxillary segment, lb = Labial segment, t1–t3: Thoracic segments; and ab1–ab10: Abdominal segments.

Check Your Progress

23. What is zygote?
24. Define the term ovulation.
25. Distinguish between monospermy and polyspermy.
26. Write the steps of fertilization.
27. Name the events that occur after fertilization.
28. What do you mean by gastrulation?

4.6 VARIOUS TYPES OF LARVA, PUPA AND THEIR SIGNIFICANCE

After embryonic development and egg hatch, neonates or immature stages of insects come out. These neonates are known as larvae in case of holometabolous insects. Development process of larvae and pupae is also called as postembryonic development. Various growth phases beginning from egg, through development of larvae to emergence of adult from pupae are variable in insects. Therefore in this section, we will learn about various types of larvae and pupae and their significance.

4.6.1 Larva

Insect emerged from hatching of egg can be a larva or nymph. All immature stages of holometabolous insects are called as larvae. Examples are butterflies, flies and beetles. True larvae are distinct from final adult stage while nymphs are more closely appear as adult. Forms of larva vary with different insects which are explained below:

I. Types of Larvae

Larvae in different orders of insects are known by different names. Larvae of butterflies and moths are called as caterpillars. Larvae of flies and beetles are called as maggots and grubs respectively. There are four types of larvae on basis of development of appendages. These are protopod, polypod, oligopod and apodous larvae (Refer Figure 4.41).

i. Protopod Larva

In protopod larva, larvae come out from eggs which have very less amount of yolk and this occurs during early stages of embryonic development. There is no segmentation on the abdomen. Thoracic appendages and head (cephalic) are primitive in form. Examples are endoparasitic larvae of wasps.

ii. Polypod Larva

The polypod (eruciform) larva has abdominal prolegs along with thoracic legs. Generally, this type of larva is poorly sclerotized and is a comparatively inactive form living closely with its food (Refer Figure 4.41A, B and C). This type of larvae is found in butterflies, scorpionflies, sawflies. These larvae are relatively inactive and are generally phytophagous.

Forms of Polypod Larva

On basis of number and location of prologs, lepidopteran (butterflies) larvae are further classified into three types: caterpillar, semilooper and looper (Refer Figure 4.41A, B and C).

- Caterpillar (eruciform) has soft body that can grow rapidly between moults. It has five pairs of prolegs which are present on 3rd, 4th, 5th, 6th and 10th abdominal segments and three pairs of thoracic legs. Examples are larvae of gram pod borer and Lemon butterfly.
- Semilooper larva has three pairs of thoracic legs and three pairs of prolegs which are present on 5th, 6th, and 10th abdominal segments. Examples are Cotton Semilooper and Castor Semilooper.
- Looper larva has three pairs of thoracic legs and two pairs of prolegs present on 6th and 10th abdominal segments, for example Cabbage looper.

iii. Oligopod Larva

Oligopod larva is the least modified form of larvae relating to adult morphology. Oligopod larva is hexapodous with a well-built head capsule and mouthparts as similar to those of adult. This type of larva has no compound eyes. Oligopod larvae do not have abdominal prolegs. But they contain functional thoracic legs and often prognathous mouthparts. Several oligopod larvae are active predators, but some are slow-moving detritivores living in soil or are phytophagous.

Types of Oligopod Larva

Generally, there are two forms of oligopod larvae namely campodeiform and scarabaeiform larvae (Refer Figure 4.41 D and E).

- A campodeiform larva is well sclerotized, dorso-ventrally flattened and is a long-legged predator with a prognathous head. Campodeiform larvae are found in some beetles, lacewings, caddisflies and twisted-wing parasites.
- A scarabaeiform larva is chubby with a poorly sclerotized thorax and abdomen. Scarabaeiform larva is short-legged, sedentary and burrowing in wood or soil. Scarabaeiform larvae are found in some other beetles and Scarab beetles.

iv. Apodous or Apod Larva

The apodous larvae have no legs and poorly sclerotized cuticle. Apodous larvae have no true legs and are worm-like or maggot-like in appearance. They dwell in soil, mud, dung, decaying animal, plant matter and inside bodies of other organisms in form of parasites or parasitoids. Usually apodous larvae have a well-developed head. These are found in stinging wasps, fleas, mosquitoes and several beetles.

Forms of Apodous Larvae

There are three forms of apodous larvae that are varying with respect to degree of sclerotization of head capsule. These are eucephalous, hemicephalous and acephalous (Refer Figure 4.41 F, G and H).

- Eucephalous larvae have a well-sclerotized head capsule and present in mosquitoes, jewel beetles and longhorn beetles and stinging wasps.
- Hemicephalous larvae have a reduced head capsule that may be retracted within the thorax and examples are Crane flies and Brachycera flies.
- Acephalous larvae do not have a head capsule and are found in maggots of Cyclorrhapha flies.

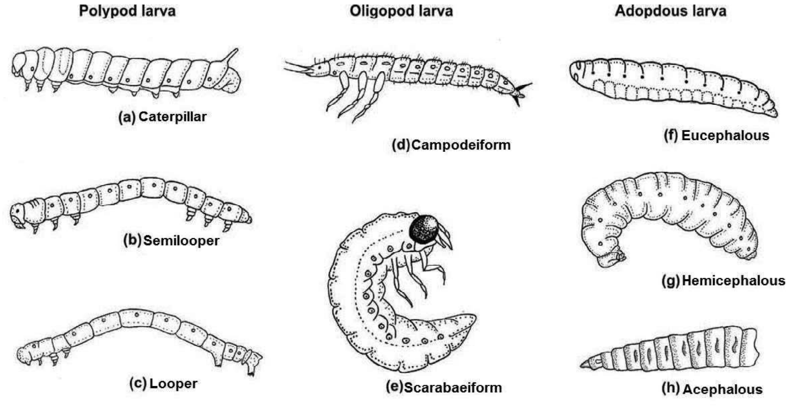

Fig. 4.41 *Different Types of Insect Larvae*

The above Figure 4.41 shows different types of insect larvae in A. Lemon butterfly, B. Cotton Semilooper, C. Cabbage Looper, D. Ladybird beetles, E. Scarab beetles, F. common wasps, G. Crane flies; and H. House flies. Sclerotized parts marked with small dots or specks.

Heteromorphosis

Heteromorphosis is type of larval development which involves radical change in larval forms between successive larval instars. It is common in parasitic and predaceous insects, such as some wasps where change in habit occurs during development of larvae. There are two types of heteromorphosis:

- **First Form of Heteromorphosis:** In this, form of first instar larva is an active campodeiform larva. For example, blister beetles (*Meloidae*), the larva hatches as free-living campodeiform which can actively search for food. After locating the food source, the larva soon molts to second stage, i.e., eruciform (caterpillar like). Further, it has to pass through either two or more additional larval instars, where it may remain as eruciform or become scarabaeiform. This form of heteromorphosis is also found in Telephone-pole beetle.
- **Second Form of Heteromorphosis:** It is found in some endoparasitic insects, such as flies and wasps. In parasitic wasps, the first instar larva is called as a protopod larva. For example, the first instar larva of braconid wasps has a large head, small unsegmented body and tapering tail. Whereas, the third instar larva is a eucephalous type of wasp larva.

II. Significance of Larva

There are several significances of an embryo developing into larva rather than directly developing into adult. It helps insect to overcome various difficulties. These are followed as:

- **Feeding:** During developmental stages, larvae consume more food to fuel up their transition into adult form. In some insect species immature forms are totally dependent on adult forms for feeding, such as in social insects, for example bees, wasps and ants.
- **Avoidance of Competition**: Advantages of larvae include the avoidance of competition for resources with adults and thus reduction of mortality of insects. Diets and life pattern larvae are quite different from those of their adults. But nymphs usually eat the same food as well as coexist with their adults. Therefore, competition is occasional among larvae and their adults. But it is likely to be predominant among nymphs and their adults.
- **Adapted to Different Environments:** The larval forms are adapted to different environments than of adults. For example, larvae of mosquitoes live almost exclusively in aquatic environment during their developmental stages and live outside water after metamorphosing into adult forms. Such adaptations in distinct environments are for their protection from predators and to avoid competition for resources.
- **Best Organized to Suit its Environment:** Hatchling (newly hatched larvae) need to obtain food but due to its smaller size is unable to feed itself the same way as an adult does. Also, it will be unable to make an effective use of defense mechanism as done by adult. Thus, new organization of

freshly emerged larvae enables an animal to avoid such hazards. It provides a mode of life which is better suited to newly emerged small larvae.

- **Aquatic Forms:** Another advantage is that larva can be able to exploit an entirely different environment because its organization is very different from that of the adults. Thus, a terrestrial adult has aquatic larval form, such as in dragonflies and damselflies; a flying adult has burrowing larvae as in flies and an adult can have free-living larvae in caddisflies.
- **Endoparasitism:** Larval stage is of great advantage for endoparasitic insects, such as some wasps, which, once inside a host, cannot transfer to another. Thus, endoparasitic insects emerge as adult from parasitized hosts after completion of larval development inside host.
- **Development of Reproductive Organ:** As adult stage of butterflies, Mayflies and stoneflies do not feed, the process of yolk accumulation, i.e., vitellogenesis is completed in late larval or pupal stage. A period of oocyte maturation occurs in adult of most insects before oocytes are prepared for ovulation.

II. Larval Growth

- **Instar and Stadium**: When insect grow in size, removes its skin one or more times, this process is called as moult or ecdysis, the sloughed skin is known as the exuviae. Intervals between the ecdysis are called as stages or stadia. Successive form produced by an insect during a specific stadium is known as instar. Once an insect ecloses (emerge as an adult from the pupa) from egg it is called as its first instar: at the last of this stadium the first ecdysis takes place and insect then enter in its second instar and so on.
- **Growth:** There is a continuous increase in weight through all successive larval stages. Weight increases progressively during development of a larval instar and slightly decreases during moulting because it losses cuticle and some water that is not displaced as they do not feed during moulting. After moult, weight of insect increases fast and weight is more compared with previous stage. Relative growth rate is equal to increase in weight related to present weight in a definite period of time and is usually declines as insect increases in size.
- **Prepupa:** Near the end of larval period, insect prepares itself to be transformed into the pupa and normally making a cocoon or other form of protection. Thus last instar larva remains quiescent for 2-3 days after which it undergoes ecdysis to from a pupa. During this part of time, stage of insect is called as a prepupa. However prepupa does not exhibit any remarkable morphological stage from that of last instar larva.

4.6.2 Pupa

After completing larval growth and development through moulting at each instar, pupal stage is formed. Pupa is a resting and inactive stage of insects with holometabolous development. Moulting period of last stage larvae into pupae is called as pupation. At end of pupal period, it is look like a fully developed adult within cuticle of pupa called as a pharate (covered) adult. Usually, there is a protective cell or cocoon that encloses pupa and later pharate adult. Some insects, such as beetles, flies, butterflies and wasps have unprotected pupae.

Types of Pupa

Generally three types of pupae are recognized according to presence or absence of functional mandibles which is used by adult to emerge from cocoon or pupal cell. These are exarate, obtect and coarctate pupae (Refer Figure 4.42).

1. Exarate or Free Pupa

In exarate or free pupa, the appendages, such as the wings and legs extend freely from body. This type of pupa is more able to move than other types (Refer Figure 4.42 A, B and C). Most pupae are exarate and found in Lacewings, Scorpionflies, Bettles, Caddisflies, Jaw moths and wasps.

Types of Exarate Pupa

Two types are recognized based on presence or absence of articulated mandibles in pupa, i.e., as follows:

- **Decticous Pupae:** When pupae have articulated mandibles are known as decticous pupae. These pupae contain apodemes fitting tightly inside adult mandibular apodemes. Therefore, pupae are moved by mandibular muscles in pharate adult stage so as to cut through cocoon. Decticous pupae are always exarate pupae (Refer Figure 4.42 A). These pupae are found in alderflies, lacewings, caddisflies and some butterflies.
- **Adecticous Pupae:** Another type of pupae has immobile mandibles is called as adecticous. In adecticous pupae, adult first loses pupal cuticle and then escape cocoon by using its mandibles and legs. Adecticous pupae are either exarate or obtect pupae. Adecticous exarate pupae are found in flies (Cyclorrhapha), fleas and most beetles and wasps (Refer Figure 4.42 B, C).

2. Obtect Pupa

In obtect pupa appendages, such as wings and legs are firmly glued down to body by moulting fluid secreted after final larval ecdysis. Generally, obtect pupae are heavily sclerotized as compare to exarate pupae. Obtect pupae are found in all butterflies, Brachycera flies and in rove beetles and ladybird beetles (Refer Figure 4.42 D and E). Obtect pupae of ladybird beetles and many nematoceran flies do not cocoon. Obtect pupae in most butterflies have cocoon and then emergence from cocoon occur either by movement of backward directed abdominal spines or a projection on head or occasionally assisted by a fluid which dissolves cocoon's silk. In nematoceran flies, butterflies and in a few beetles and wasps, pupae are of adecticous obtect type.

3. Coarctate Pupa

In some dipteran flies, such as botfly, skin of last instar larva is retained so as to cover pupa and become hardened. It completely separated from insect which it surrounds. This type of pupal casing or capsule is called as a puparium and pupa protected in this manner are called as coarctate. Puparia are cylindrical or barrel like in shape and they do not appear externally that the developing insect inside (Refer Figure 4.42C).

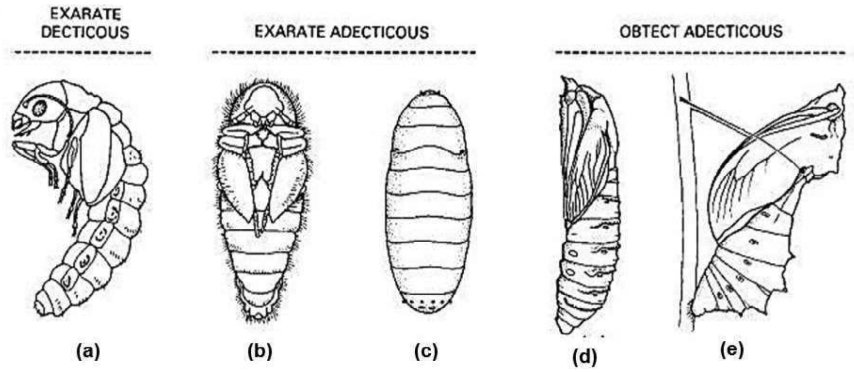

Fig. 4.42 *Types of Pupa found in, A. Alderfly, B. Skin Beetle, C. Blow Fly Pupa within Puparium, D. Cossid Miller Moth; and E. Swallowtail Butterfly*

II. Significance of Pupa

- **Acts as Transitional Phase:** During pupal period, the insects are not able to feed and become quiescent. It is considered as an acquired transitional phase throughout which the larval body structure and organs are modified so as to adapt them to the necessities of the upcoming adult or imago. Usually, pupae are motionless, but several pupae have a restricted ability for locomotion that is apparent around the end of the stadium, so to enables the emergence of the perfect adult insect.
- **Diapausing Stage:** For many insects, pupa is also the stage in which an insect survives adverse conditions by means of diapause. Diapause is arrested development of insect stage. This is generally initiated or terminated by **photoperiod,** thermoperiod, temperature, moisture, food quality, crowding, or some combination of these factors. Diapausing insects in pupal stage can be more tolerant to food shortages, adverse environments (temperature or moisture), or toxic chemicals. This tolerance can allow diapausing insects, such as stored-product insects to better survive in unfavourable conditions.
- **Protection During Adverse Condition:** An immobile pupa is susceptible to attack by predators or parasites and to changes in climatic conditions. As pupal stadium last for a large time, thus to obtain protection against such adversities pupa has a thick, tanned cuticle. Also, in many insects it is enclosed within a cocoon or puparium or earthen cell constructed by last larval instar. Cocoon has various kinds of extraneous material, for example, soil particles, small stones, leaves or other vegetation, or can be made solely of silk. It obtains additional protection by taking on color of its surroundings. Many parasitic insects remain within, and are thus protected by host's body in pupal stage.
- **Time-Limited Ecological Vulnerability:** Growth is largely confined to larval stage, while most development occurs in pupal stage. The growth rate during larval life is maximized at cost of food processing efficiency. In case of food plants, these resources can be temporary because of a short growing season or the development of plant defenses. This time-limited ecological vulnerability is likely to be favour in development of non-feeding pupa stage where development of adult can occur. Emerged adult can escape

from limited resource area and migrate to other place where food is plentiful. Thus pupal stage can be advantageous in reducing or eliminating that period in which larva is sensitive to complete loss of fitness through early death.

- **Defense Mechanisms:** Pupae are immobile stages that face a number of challenges, including predation and infection. Pupae have evolved different anti-predator defense mechanisms, such as crypsis. Internal re-organization required by complete metamorphosis faces an additional problem to the developing insect as escape of microbes from inside of gut into insect's haemocoel. In butterflies, host upregulates expression of lysozymes and other immune effectors during pupation and before adult moult. In hemimetabolous cricket, no such upregulation is found.
- **Competition:** The primary advantage of complete metamorphosis is eliminating competition between different stages that is larva, pupa and adult. Three separate life stages are adapted for two reasons: i. it facilitates stage-specific resource (food, etc.) utilization and structural specialization, such as adaptation of different sets of mouthparts for alternative food sources; and ii. it encourages population growth by reducing intraspecific competition between stages.
- **Reconstruction of Adult Organs:** During pupal stage, most of inner (anatomy) and outer (morphology) modifications and reconstruction take place. Significance of pupa is apparent in wing development and related modifications for formation of adult. As in life cycles of some female Coccid beetles lack pupal stage and thus are wingless and larviform. Male Coccid beetles have a pupal stage and are winged insects.

III. Pupa Protection and Development

1. Pupa Protection

As pupae have very restricted ability of movement and no mechanisms of defense, some means of protection are needed. Followings are the structures, in which pupae are encased and thus are protected:

- **Earthen Cells:** Several butterflies and beetle larvae dig beneath ground and then create earthen cells in which they pupate (Refer Figure 4.43A).
- **Silk Cocoon:** Numerous insects use only silk to construct their cocoons. Examples are some Lacewings, many Butterflies and wasps. Large variations occur with respect to colour, type of silk, texture and form of cocoons. The thickest and most perfect form of cocoon occurs in the Saturniid moths (Refer Figure 4.43B).
- **Puparium:** Puparium is a special protective structure is formed from the cuticle of last instar larva (for example flies). Process of puparium formation is called as pupariation. After apolysis, head and appendages of pupa or adult are concealed underneath epidermis of larva and pupal cuticle is released (Refer Figure 4.42C).
- **Silk Pad:** A small number of insects have unprotected pupae that are suspended from a silk pad. This type protection of pupa is found in some butterflies, such as Monarch butterflies (Refer Figure 4.43C).

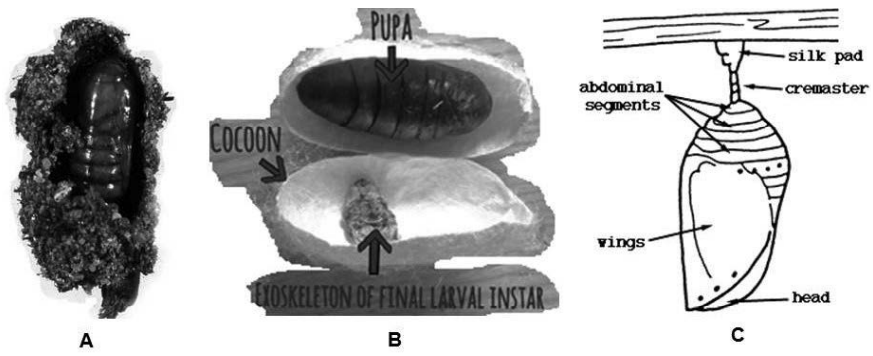

Fig. 4.43 *Pupa in A. Earthen Cell of Moth, B. Cocoon of Saturniid Moth; and C. Silk Pad of Monarch Butterfly*

2. Movement in Pupa

- Pupae of some lacewings recover some movement before the last moult and are able to crawl.
- Some Caddisflies display adaptive modifications to allow them to swim to water surface and then results in exit of adult insect.
- Pupae of *Culex* mosquitoes and some midges are usually active during entire development period and are able to actively swim through caudal movements.
- Several pupae occur in soil, wood or stems exhibit less pronounced movements. In such cases, pupae are usually provided with spines or denticles which enable their movements outward, when the time is near to emergence of the adults.

3. Development During Pupa Stage

- **Imaginal Disc:** Organs of larva usually have cells with hidden embryonic capability that afterward involved in forming parts or structures of adult. These persisting embryonic regions are known as imaginal primordia. An imaginal primordium is called as imaginal disc when it has completely lost connection with larval cuticle and stops to form larval cuticle.

  Imaginal disc is infolded below epidermis of larva, developing a cavity called as peripodial cavity. Peripodial cavity is lined with peripodial membrane. When imaginal disc expands appendage develops and drives into cavity, thus turn out to be folded as it increases in size (Refer Figure 4.44).
- **Evagination and Hormone Regulation:** Evagination is a process of turning outward, it takes place due to a reordering of cells in imaginal disc and by the same time, it tends to rise in surface area. This event initiate through an increase in ecdysone hormone in insect haemolymph. In larval moults, if amount of this hormone increases, evagination is blocked through Juvenile Hormone. Usually larva and nymph undergoes a specific number of instars during their growth period and ultimately move in metamorphosis once they attain the species-specific threshold size. Juvenile Hormone (JH) is found during most of larval/nymphal growth however disappears at the last instar as they get ready for metamorphosis.

- **Reconstructions:** During pupa stage, the adult appendage is turned outwards (evagination). Generally, major modification occurs during metamorphosis for development of muscular system. Central nervous system of holometabolous insects is broadly restructured at metamorphosis. In holometabolous insects, sensory system for adult can be completely renewed during metamorphosis. Alimentary canal is widely modified during pupal phase in holometabolous insects. Occasionally malpighian tubules of larva continue as unmodified in the adult or very small modifications can take place. In wasps, larval Malpighian tubules are completely histolyzed and being replaced by new tissues developed from tip of proctodeum (fore gut).

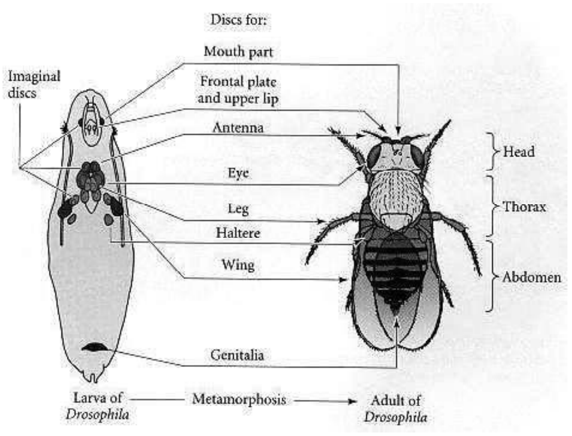

***Fig. 4.44** Locations and Developmental Fates of Imaginal Discs in Fruit Fly (Drosophila melanogaster)*

4. Eclosion of Adult from Pupa

On completion of pupa period, adult escaping from cuticle of the pupa is known as eclosion. When the pupa is enclosed in a cell or cocoon the adult also has to escape from this. Newly emerged adult has soft cuticle. Thus it allows expansion of body parts through taking air from outside into tracheal sacs and enhancing haemolymph pressure via muscular activity. Usually, the wings fall downward so as to assists their inflation. Accumulation of pigment in cuticle and epidermal cells takes place only earlier or later emergence due to action of neurohormone bursicon. After adult emerge through pupal cuticle, several holometabolous insects release a faecal fluid known as meconium. Meconium is metabolic wastes which are collected throughout pupation period.

Check Your Progress

29. What is postembryonic development?
30. Define the term larvae.
31. Name the different types of larvae.
32. What do you mean by heteromorphosis?
33. What is pupa?
34. Write about the types of pupa.
35. List the significance of pupa.

4.7 METAMORPHOSIS IN INSECTS

Post-embryonic development is divided into a series of immature stages in which each stage is distinct from the next one through a moult. Thus anatomical and morphological change in forms of immature stages to form adult (or imago or imaginal) is known as metamorphosis. Process of metamorphosis varies with different insects. Therefore, it is necessary to understand various types, theories and importance of metamorphosis in insect life.

4.7.1 Types of Metamorphosis

Metamorphosis is divided into two main groups: Heterometabola and Holometabola.

1. Heterometabola: Heterometabola occurs in Exopterygote insects (have external wing growth), which pass through a simple metamorphosis. Thus it is direct or incomplete metamorphosis. A pupal stage is absent and immature insects are called as nymphs. The nymph which hatches from the egg has a general resemblance to the adult in body form, type of mouth parts and possession of compound eyes, though these nymphs may have adaptations associated with their particular habits of being aquatic, swimming or burrowing.

In these the change from nymphs to adults is a gradual process in which appendages, mouth parts, antennae and legs of the nymph grow directly into those of the adult.

Wings develop gradually as external outgrowths of thorax and are visible externally in the nymphal instars, because of their external wing development they are also called exopterygota. The reproductive organs mature gradually. Insects showing this slight change from nymph to adult are known as heterometabolic (gradual), they include Dictyoptera, Orthoptera, Isoptera, Hemiptera and Anoplura.

Though nymphs of dragon flies, may flies, etc., are quite different from the adult in having special nymphal adaptations because their nymphs are aquatic, while the adults are aerial, the nymphal adaptations are shed in changing into adults, such forms with slightly greater changes are called hemimetabolic (incomplete), they include Odonata, Plecoptera and Ephemeroptera.

2. Holometabola: Holometabola occurs in Endopterygote insects (wings form internally), which pass through a complex metamorphosis. In this, the young are larvae and adult is preceded by a pupal instar. Hence, this is also known as indirect or complete metamorphosis.

In Lepidoptera, Coleoptera, Hymenoptera, Diptera, Siphonoptea, etc., the young which hatches from the egg is called a larva, the larva is very different from the adult in structure, body form, mouth parts, legs and in its mode of life, the larva has lateral ocelli in place of compound eyes, it feeds voraciously, grows, moves about and undergoes ecdyses.

The larva is so different from the adult that it first changes into a resting, quiscent instar called a **pupa** which is often enclosed in a cocoon secreted by the labial glands of the larva. Great transformation occurs in this instar, wings develop internally from pockets of the hypodermis, and they are not visible from outside.

Because wings develop from internal imaginal discs these insects are also called **endopterygota**. Appendages are formed, muscles, tracheae and parts of the alimentary canal are replaced by corresponding organs of the imago. Such vast changes are called holometabolic metamorphosis.

In holometabolic insects there is an internal reconstruction during late larval and pupal instars. Larval organs, with the exception of central nervous system and developing reproductive organs, are disrupted, their breaking down is called histolysis, this is brought about by phagocytes which feed on the organs, and products of their digestion are then used for building new structures.

The building of new structures is brought about by growth centres called **imaginal buds** or **discs**. Imaginal discs are groups of formative cells which are set aside in the larva, they are the rudiments of future organs of the imago, they form legs, mouth parts, internal organs and wings.

This process of formation of organs of an imago from imaginal discs inside the pupa is known as **histogenesis** and it results in the formation of the imago.

Thus, two postembryonic processes occur in all insects, the first is growth in the young and the second is metamorphosis, in both of which moulting takes place; both processes are controlled by hormones of endocrine glands. Insects have two such endocrine glands, they are corpora allata and prothoracic glands.

The juvenile hormone of corpora allata controls growth and moulting up to the end of the larval period. So long as the juvenile hormone of corpora allata is produced the final moulting into a pupa or into an adult cannot take place.

The prothoracic glands are a pair of small glands in the first thoracic segment, they produce a hormone called **ecdyson** which brings about moulting and development of imaginal discs and reproductive organs.

When both hormones are secreted, then moulting of the larva only will take place. The result of the two hromones is supression of adult characters from appearing during larval and pupal instars. When only ecdyson is secreted, and the juvenile hormone is not produced, then the larva will moult into a pupa, and the pupa into an imago.

Thus, it is seen that ecdyson is essential for each moulting, but its action is modified as long as the juvenile hormone is present. Removal of the old cuticle in ecdysis is brought about by an enzyme secreted by the hypodermis, the enzyme erodes the lower surface of the cuticle, and then the hypodermis secretes a new cuticle below the old one.

Thus, there are four patterns of growth and development in insects namely ametabolous, paurometabolous, hemimetabolous and holometabolous. These are explained below in detail,

i. Ametaboly: No Metamorphosis

Ametaboly is the basic and most primitive pattern of insect development in which there is no metamorphosis. Immature stage emerged from egg is very similar to adult except that it lacks sexual organs. It grows only in size by replacing its old skin through moulting. Larva grows bigger and genitalia develop progressively with each moult. Young one which emerges from egg resembles adult in miniature form, is called as **nymph**. Reproductive organs are undeveloped in nymph. Nymph after moulting becomes an adult. Both nymphs and adults live in the same habitat. Ametaboly occurs in the primitive and wingless insects (Apterygotes). For example, adults of bristletails, springtail and silverfish keep on moulting even after attaining sexual maturity.

Ametaboly in Silverfish: Silverfish hatched from egg looks like an adult and undergoes anatomical changes between moults (Refer Figure 4.45). Immature silverfish moults 6-7 times until it reaches sexually mature adult stage. In favorable conditions, silverfish may typically continue to moult during its lifespan and moults 25–66 times.

ii. Paurometaboly: Gradual Metamorphosis

Paurometaboly is the type of development, which occurs in less primitive insects like cockroaches, grasshoppers, praying mantis and white ants. Postembryonic development and growth is gradual, and not having any striking morphological changes. Distinctive feature of this type of metamorphosis is the acquisition of wings.

In this, the newly emerged young one closely resembles adult in general body form, habits and habitat. But many adult features like wings and reproductive organs are not developed and their relative proportions of body also differ. The young forms are called as nymphs. Wings develop as wing pads on second and third thoracic segments at an early stage and gradually increase in size during each successive moult. External genitalia also develops gradually after each moult. These nymphs lead an independent life and attain adult features through several molts. There are three stages in life cycle of these insects that is egg, nymph and adult but pupal stage is absent.

Paurometaboly in Grasshoppers: In grasshoppers, before becoming adults the nymphs undergo 5-6 moults to change their body form (Refer Figure 4.45). The nymph stage is species specific and lasts for a period of 5-10 days depending upon weather conditions like temperature and humidity.

Paurometaboly in Cockroaches: Immediately after hatching, nymphs undergo first moulting or ecdysis and then 6 or 7 successive moults occur. As nymphal development proceeds, wing pads arise, body increases in size, colouration becomes darker and ultimately adult takes its form with fully developed wings and genitalia. Thus development of cockroach is simple and direct. It has incomplete or gradual metamorphosis known as Paurometaboly.

iii. Hemimetaboly: Incomplete Metamorphosis

In this type of development, adult form is attained by gradual morphological changes with successive moults (Refer Table. 4.2). The hatched larva lacks wings and genitalia but have some other characteristic features which are absent in adult. These features are lost at the final moult. Insects have aquatic larval stages are Stoneflies, Mayflies, and Dragonflies (Refer Figure 4.45). The young forms are known as naiads which are aquatic and respire by external gills but adults are terrestrial in behaviour. Their life cycle also involves three stages: eggs, naiads and adults. When naiads are ready to transform into adults, they come out of water and adult winged forms are released. The wings and genitalia develop externally but are not fully formed till adulthood. After formation of wings, no further moulting takes place. Exception occurs in mayflies where winged forms of aquatic nymphs come out and rest on trees to undergo final moulting to become adults.

Table 4.2 *Difference between Paurometaboly and Hemimetaboly*

S.No.	Paurometaboly	Hemimetaboly
1.	Nymphs occupy the same environment as the adults.	Nymphs, called naiads occupy aquatic habitats while adults are terrestrial.
2.	It occurs in Cockroaches, Grasshoppers, Praying mantis.	It occurs in Stoneflies, Mayflies, and Dragonflies.
3.	Distinctive feature of this type of metamorphosis is the acquisition of wings and developed reproductive organ.	Since naiads live in water, while adults are aerial, their differences are of an adaptive nature and principal concern is respiratory system.
4.	It is not having any striking morphological changes.	Morphological changes which take place are greater than in the Paurometabola.
5.	Newly emerged young one closely resembles adult in general body form.	Transition from nymph to adult is more profound.

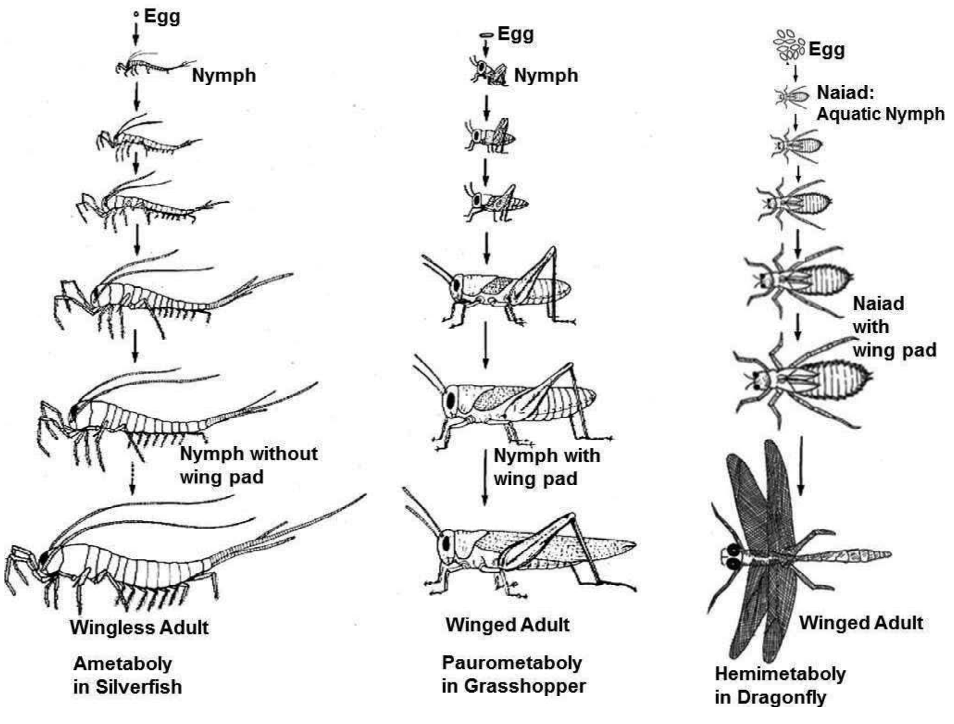

Fig. 4.45 *Types of Incomplete or Direct Metamorphosis in Different Insects*

Subtypes of Hemimetabolous Development

- **Prometaboly:** Post-embryonic development of mayflies (Ephemeroptera) undergoes in a series of nymphal stages similar to adult but without developed wings. Last instar nymph transforms into a subimaginal stage that has functional wings but without reproductive capabilities. This stage is developed into the perfect adult that is winged and reproductively capable. This particular development is called as prometabolan (Refer Figure 4.46).
- **Neometaboly:** Some hemimetabolous groups, such as thrips and some hemipterans, have independently evolved a holometabolous-like lifestyle. This particular life cycle with a quiescent stage in between nymph and adult stage is known as neometabolan (Refer Figure 4.46).

  Several thrips (Thysanoptera) and whiteflies (Hemiptera) have an essentially hemimetabolan development but include one to three quiescent stages, which are reminiscent of holometabolan pupal stage.

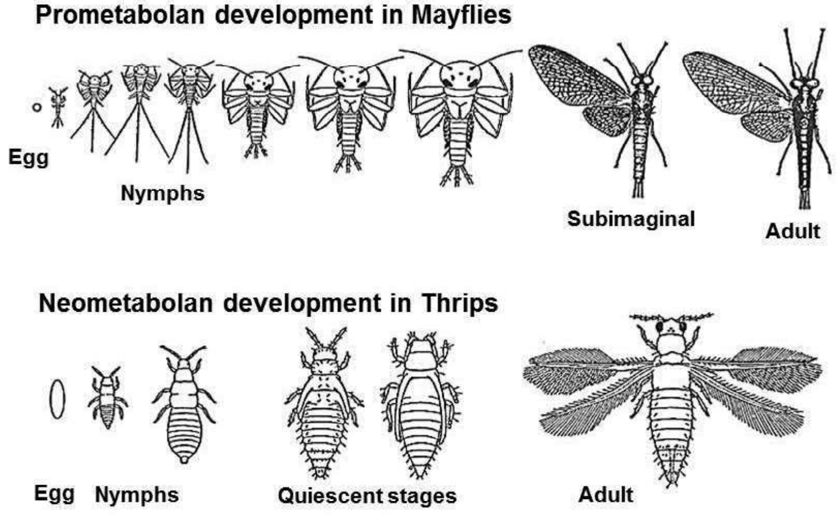

***Fig. 4.46** Subtypes of Hemimetaboly: Prometaboly in Mayflies and Neometaboly in Thrips*

iv. Holometaboly: Complete Metamorphosis

Complete metamorphosis is a kind of morphological change during post-embryonic transformation in which larva has no similarity with adult and there is always a pupal stage. Complete metamorphosis takes place in beetles (Coleoptera), flies (Diptera), wasps (Hymenoptera) and butterflies and moths (Lepidoptera). In holometabolous insects, transition from larva to adult takes place through non-feeding, transitional stage known as pupa. After completion of last larval instar, insects undergo pupal stage. During pupation, anatomical and morphological development of adult takes place. At end of pupation, an adult emerges through pupal cuticle case.

- In butterflies and moths, the larva is known as caterpillar (Refer Figure 4.47). Caterpillar has a distinct head with powerful mandibles and three pairs of jointed thoracic legs. Abdomen of caterpillar has four or five pairs of un-jointed, short abdominal legs which are known as pseudo-legs or prolegs. These caterpillars eat voraciously and grow rapidly with several moultings. After completing four or five moults, the caterpillar is transformed into pupal stage.

- In houseflies and other flies, the larva is worm-like and devoid of appendages and is known as maggot (Refer Figure 4.47). The mature larva is about 12 mm long. The head is indistinct, with a pair of oral lobes and hooks.
- In beetles, such as ground beetles and ladybirds, larval morphology is highly varied among species. Larva has well-developed and sclerotized heads, distinguishable thoracic and abdominal segments and are known as grubs.
- In bees and wasps, the larvae are grub-like with well-developed head and mouthparts are of chewing type. Larvae are generally apodous, rarely eruciform with locomotory appendages.

Holometaboly in Honey Bee: Brood is defined as whole pre-imaginal period (eggs, larvae and pupae). Egg and early larval stages live in uncapped brood cells. Last two days of larval stage, pupal stage and first half-day of adult stage occur under capped brood cells (Refer Figure 4.47). Honeybee undergoes through five larval instars.

During first three days after hatching, all larvae are fed only with royal jelly. Within three days, weight of larvae increases from 0 .1 to 5 mg, i.e., by a factor of 50. Larvae that will become future queens are fed ten times more than are larvae reared as workers. After two and a half to three days, a worker larva is no longer capable of being reared as queen. After workers have covered cells with a convex cap of wax (more convex for male brood), larvae cannot receive further food. Within 36 hours after cell capping, larva spins a cocoon and defaecates. After metamorphosis, young adult emerges by chewing away cell cap.

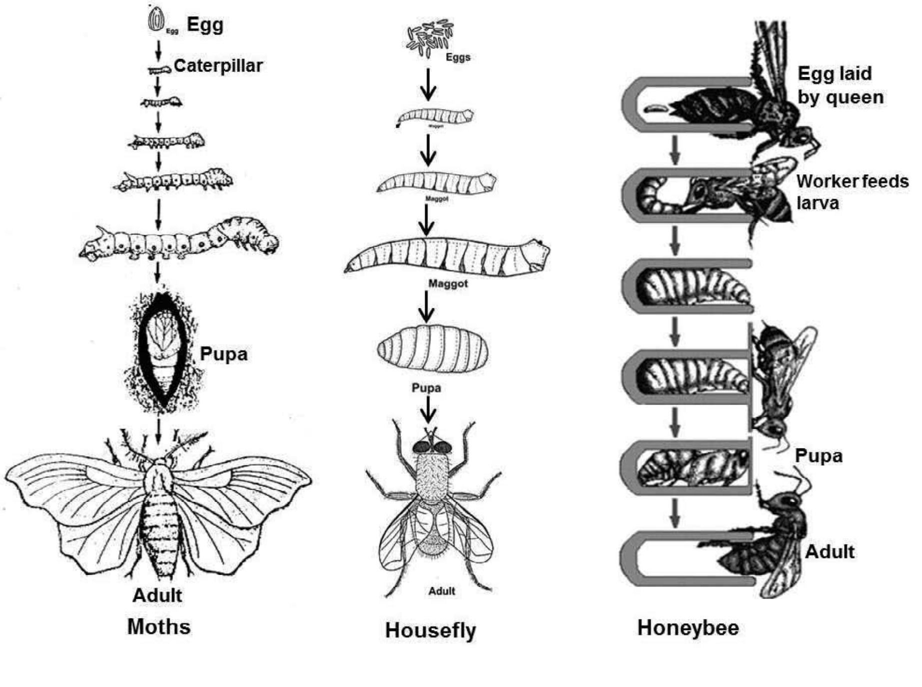

Fig. 4.47 *Holometabolous Development in Different Insects*

4.7.2 Theories of Metamorphosis

Scientists have studied that arthropods with various life histories (cycles) evolved from their ancestors. According to this, there are generally three theories that indicates evolution of insects with different life histories. These theories revealed following facts:

- Arthropod groups have monophyletic origin, i.e., they have evolved from a common ancestor.
- Arthropods groups are diphyletic, i.e., two main subdivisions of groups evolved from common ancestor.
- Each major group evolved autonomously of the other, i.e., groups have a polyphyletic origin.

Followings are the positive and negative features of various theories about different insect life histories and metamorphosis:

1. Monophyletic and Diphyletic Theories

Proponents of Monophyletic theory argue that plenty of features are similar to arthropods and many of these resemblances might not have been accomplished other than a common origin. Monophyleticists further point to extremely conserved feature of main arthropod forms and developmental processes through which these groups are produced, such as chemistry of cuticle and process of molting, the formation and impeccable structure of compound eyes and head development during embryogenesis. There is also continuously increasing proofs from study in molecular biology of insects, not all but most of these follows the monophyletic concept of insect development.

Haeckel (1866) conceived a first monophyletic system for describing arthropod evolution. Based on the fact that the arthropod groups evolved from a common ancestor, he categorized arthropods into two categories namely; i. the Carides, i.e., Crustacea including Xiphosura, Eurypterida and Trilobita; and ii. the Tracheata, such as Myriapoda, Insecta and Arachnida. By identifying that *Peripatus* (Onychophora) possessed most of the features of arthropoda, such as tracheal system, Moseley (1894) envisioned this genus to be the ancestor of the Tracheata group, with the Crustacea being evolved autonomously. From here the first scheme of diphyletic theory for arthropods evolution was proposed.

On contrary of it, monophyleticists considered mandibles of the crustaceans, myriapodas and hexapods as homologous in origin. Supporters of mandibulata concepts, for example Matsuda (1970), derived insect leg from ancestral crustacean form, through suggesting that the extra segments were merged into the thorax as subcoxal parts.

Wheeler and his associates studied and compared more than hundred morphological characters and sequences of rDNA with subunits 18S and 28S, and polyubiquitin in about 30 taxa of arthropods, Onychophora, Annelids and a Tardigrade. Through these findings they revealed the unambiguous conclusion that the arthropod groups are of monophyletic origin.

2. Polyphyletic Theory

Supporters of polyphyletic theory say that the almost identical characteristics of arthropods are interconnected and interdependent, i.e., these groups developed from the evolution of a rigid exoskeleton. Therefore, arthropod groups evolved through developing following features:

- To develop, arthropod group need to moult regularly.
- To exhibit movement they need to contain articulated limbs and body.
- Tagmosis is a rational outcome of segmentation and leads to formation of the nervous and muscular systems.
- The presence of cuticle requires alterations in the gas exchange, sensory and excretory systems and the open circulatory system, i.e., haemocoel is the outcome of an organism who has no longer required a body cavity associated with hydrostatic purposes.

Therefore, the polyphyletic supporters required to validate the polyphynetic nature of the cuticular exoskeleton. Polyphyletic workers state that the progressions of cuticular hardening exhibited in three arthropod groups are somewhat different, for instance, occurrence of quinone-tanning in insects, disulfide bridges in arachnids and impregnation with organic salts in crustaceans. Anderson (1973 and in Gupta, 1979) found some proofs from study of embryology in turn support the polyphyletic theory.

Overall, the current balance seems in favour of a monophyletic origin of arthropods.

According to latest phylogenetic studies (Kjer *et al*., 2006), the Endopterygota (Holometabola) are monophyletic, which suggests that the innovation of holometabolan metamorphosis appeared only once. Therefore, the most parsimonious hypothesis is to consider that the holometabolans would have originated from hemimetabolan ancestors.

3. Formal Theory of Metamorphosis

The first important formal theory about metamorphosis was written in 1651 by William Harvey. He hypothesized that embryo is forced to hatch before the complete development due to limited amount of nutrients in egg. During the post-hatch larval life, the de-embryonized animal would accumulate resources from external environment and reach pupal stage, which Harvey viewed as the perfect egg form. After this theory, studies of Jan Swammerdam pointed that larva is not a sort of egg but a transitional stage between egg and adult. He also categorized the insects in terms of four metamorphosis types, insects that grow without transformation (lice), insects that develop wings progressively without quiescent stage (locusts), insects that develop under larva cuticle through a quiescent pupa stage (butteries and beetles) and fourth group includes insects that pass pupal stage under skin of last larva stage (flies).

4. Precocious Eclosion Theory

In 1883, John Lubbock revitalized Harvey's hypothesis and argued that the origin and evolution of holometabolan development can be explained by the precocious eclosion of the embryo. According to precocious eclosion theory, hemimetabolan nymphal stages would be equivalent to holometabolan pupa. Then, Berlese (1913) proposed that the larval stage arose after the developmental events of embryogenesis were transposed to postembryonic life. To critics of this theory, as Howard Hinton (Hinton, 1948), post-embryonic development would be equivalent in hemimetabolans and holometabolans. Thus, hemimetabolan last nymphal instar would be homologous to holometabolan pupae. Between these two conceptions, other homologation systems were proposed, like that of Poyarkoff in 1914 or that of John Heslop- Harrison in 1955.

5. Endocrine Based Theory

V.B. Wigglesworth (1936) studied that corpora allata in insects affect metamorphic development. Then, he in 1954 suggested that possible role of JH was to suppress adult differentiation until metamorphosis. Wigglesworth's criticisms of Harvey/ Lubbock/Berlese concept of metamorphosis, new theories that incorporated JH into Berlese's hypothesis emerged.

J.W. Truman and L.M. Riddiford, in 1999, revitalized the precocious eclosion theory with a focus on endocrine control of metamorphosis. They postulated that hemimetabolan species hatch after three embryonic moults into a nymphal form similar to adult. On the other hand, holometabolan insects hatch after only two embryonic moults into vermiform larvae that are very different from adult. Truman and Riddiford (1999, 2002) considered that morphogenesis of holometabolan became shortened as a result of advancement of JH appearance during embryogenesis.

4.7.3. Importance of Metamorphosis

Since metamorphosis evolved, it has played very important roles in insect's life for their success on this planet. Followings are important roles of metamorphosis:

- **Eliminate Competition:** Main advantage of complete metamorphosis is eliminating competition between the young and old. Larvae and adults occupy very different ecological niches. For example, in Lepidoptera, caterpillars are engaged gorging themselves on leaves, completely disinterested in reproduction, butterflies are flitting from flower to flower in search of nectar and mates. Because larvae and adults do not compete with one another for space or resources, more of each can coexist. Ultimately, these transformations of insect life stages also reduce mortality rate and increasing survival rate.
- **Resource Utilization and Accumulation:** Insect postembryonic development has increased separation of processes in different life stages. Process of growth and accumulation of reserves are functions of larval stage. Reproduction and dispersal are functions of adult stage. This leads to spending of a greater proportion of insect's life in juvenile (larval) stage. Thus, results in an increasing degree of difference between larval and adult habits and form. This is further accompanied by modification of final larval instar into a pupa. Pupa does not feed and its energy comes from those foods reserved by its larval stage. During pupation, adult structures are formed and replace larval structures.
- **Developmental Size Thresholds:** The main difference between complete

metamorphosis and incomplete metamorphosis is that complete metamorphosis has a very active, voraciously feeding larva and an inactive and non-feeding pupa whereas incomplete metamorphosis has nymph, which resembles a miniature adult. The main adaptive benefit of complete metamorphosis is decoupling between growth and differentiation. This facilitates the exploitation of short-lived resources and enhances the probability of the metamorphic transition escaping developmental size thresholds.

- **Different Pattern of Life Cycle:** In insects with complete metamorphosis, adults and larvae do not compete for same food source, do not have same predators and occupy different habitats. However, adults and larvae do not share same food, which can be a disadvantage in food-poor environments; short adult life span; only adult has true mobility. Metamorphosis can also provide handy protection from winter, such as a hard pupal case.

  Advantage of incomplete metamorphosis, is that they do not have vulnerable pupa stage; parental protection can occur; mobility throughout life cycle. Disadvantages are that nymphs compete with adults for food and habitat; can share the same predators.
- **Adult Development:** Flight provided a means to avoid predation, to move rapidly between dispersed food patches and to undertake long-range dispersals. Therefore, metamorphosis is necessary for wing development during immature stages to form adults with flight capability. Reproductive organs and genitalia are important for adult to reproduce and increase their population. Reproduction also results in species diversification depending upon its environment and mutation capability. Reorganization of larval organs occurs during metamorphosis to form adult organs so that adult live in different environment/habitats from that of larva.
- **Species Diversification:** Adaptations of the larval and adult stages were developmentally uncoupled. This allowed evolution of a larval stage with reduced mobility but enhanced capacity to exploit food resources without affecting adult specializations for dispersal and reproduction. This life history innovation resulted in rapid diversification and radiation within Holometabola, which includes orders that have the most species (Coleoptera), the most biomass (Hymenoptera) and greatest effects on agriculture (Lepidoptera) and on human and animal health (Diptera).

Check Your Progress

36. What is metamorphosis?
37. Write about heterometabola metamorphosis.
38. What is holometabola metamorphosis?
39. Define the term histogenesis.
40. What are the facts that are derived from the various theories of metamorphosis?
41. List the important roles of metamorphosis.
42. What is neometabolan?

4.8 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Reproduction in most of the insect species is bisexual. Egg cell produced by female insect develops when fuse with the spermatozoa cell introduced by the male.
2. Insect reproductive system comprises of paired sexual gonads that is the ovaries of female and testes of male.
3. Male reproductive system in insects consists of internal reproductive organs, spermatozoa and external reproductive organs.
4. Testes usually lie either above or below gut in abdomen and are near to middle axis. Each testis has a series of testis tubes or testicular follicles. These vary in number and arrangement in different insects.
5. In many insects, seminal vesicles are dilations of vasa deferentia. In some insects, such as wasps and mosquitoes, seminal vesicles are present as dilations of ejaculatory duct. Seminal vesicles store sperm before transfer to female reproductive tract.
6. Mature spermatozoa in most insects are flagellate containing head and tail parts. The insect sperm exhibit high variation in morphology.
7. Process of conversion from primitive germ cell spermatogonium into mature germ cell spermatozoa is called as spermatogenesis.
8. Female reproductive system contains a pair of ovaries that are joined with a pair of lateral oviducts. These are fuse to lead as a median oviduct that opens posteriorly into a genital cavity.
9. Paired ovaries situated above or lateral to the gut in abdomen. Each ovary has many egg-tubes called ovarioles similar with testicular follicles of testis in male. The oocytes grow and mature in ovarioles.
10. Sexual reproduction involves several physiological events, such as mating of insects and sperm transfer, egg (oocyte) development and egg fertilization.
11. Mating behaviour of most insects can be subdivided into four parts. These parts are i. Location and recognition of a mate, ii. Courtship, iii. Pairing and iv. Copulation.
12. Pheromones are most common signal used by insects in mate location. Volatile chemical attractants are both highly specific and capable of exerting their effect over a long distance. Pheromones are produced by females and are used by both diurnal and nocturnal insects.
13. Copulation is the reproductive or mating act in which male reproductive organ, for example penis enters female reproductive organ, for example vagina. *Copulation* usually includes mounting, *intromission* (insertion of penis into vagina), and sperm discharge in to female insect.
14. Process of sperm transfer by male to female reproductive organs during copulation is called as insemination.

NOTES

15. Pre-vitellogenesis is a process where there is an increase in nuclear and cytoplasmic material in oocyte with no addition of yolk. Whereas, vitellogenesis is a process of synthesis and deposition of large amount of yolk in oocyte. Insect's eggs are both microlecithal and centrolecithal types. Thus, insect eggs have massive yolk that occupies center of egg and cytoplasm forms a thin peripheral layer around yolk. Chemically yolk is lipoprotein composed of proteins, phospholipids and neutral fats along with a small amount of glycogen.
16. Functions of yolk are as follows:
    - Yolk is also called as deutoplasm, is nutrient-bearing portion of egg and supply food to embryo at the earliest stages of development.
    - Major proteins are stored in the yolk of developing oocytes that provide a nutritional store for utilization during embryogenesis.
    - Yolk supplies energy to developing embryo.
    - It provides material for synthesis of those substances that are required for elaboration of embryonic body.
17. Most insect species are bisexual and females lay eggs that have large amount of yolk. Such insects are called oviparous.
18. In viviparity, female insect keep their fertilized eggs inside their genital tract until they develop into young ones and then these are laid. Developing embryos obtain nourishment directly from female.
19. In ovoviviparity, female insects keep their eggs in reproductive tract until before eggs are ready to hatch. These insects are called ovoviviparous.
20. Polyembryony is the development of more than one embryos from one egg. Polyembryony is found in about 30 wasp species of parasitic Hymenoptera and one species of Strepsiptera.
21. Eggs of some female insect species undergo development without fertilization of their eggs. This mode of asexual reproduction is called as parthenogenesis. Parthenogenesis is divided into two broad forms namely: thelytoky and arrhenotoky.
22. Several insects mature sexually rapidly in early life stage and thus are able to reproduce in larvae or pupae stage. This mode of reproduction is called as pedogenesis. Most of insects with pedogenesis are also viviparous and parthenogenetic in reproduction. In gall midges and wood midges (Cecidomyiidae), larvae reproduce larvae or sometimes oviposit eggs. Pupal forms of some Gall midges (*Tekomyia and Henria)* produce larvae.
23. After mating and sperm transfer in insects, fertilization of ova takes place in female insects that eventually initiates embryonic development in fertilized egg called zygote.
24. An egg gets fertilized when it moves into common oviduct and genital cavity where a few sperm are released from the spermatheca. This event of egg release is called as ovulation. Ovulation is the movement of an egg from the ovary into the lateral oviduct. This also provides stimulus to maturation of oocytes.

25. Several spermatozoa enter egg. Only one of these is usually utilized in fertilization of egg. This called as monospermy. Polyspermy is the entry of two or more sperm into an egg and is common in insects. But only one sperm normally undergoes transformation into a pronucleus and the rest of sperm degenerate. In fruit flies, some eggs are monospermic and many eggs receive 30 or more spermatozoa and thus are polyspermy. But in some insects, several female nuclei are found. For example, butterflies and moths have binucleate eggs and thus each is fertilized by a different spermatozoon.
26. The process of fertilization can take place in following steps:
    - Sperm capacitation
    - Sperm entry to egg
    - Sperm penetration
    - Ovum activation
    - Amphimixis
27. After fertilization of eggs in female body, fertilized egg deposited, and then embryonic development begins with first mitotic division of zygote nucleus and terminates at hatching.
28. Gastrulation is process of invagination and proliferation of cells along midline in egg. During gastrulation, single-layered germ anlage develops into two-layered germ band. Germ band elongates and becomes broader.
29. After embryonic development and egg hatch, neonates or immature stages of insects come out. These neonates are known as larvae in case of holometabolous insects. Development process of larvae and pupae is also called as postembryonic development. Various growth phases beginning from egg, through development of larvae to emergence of adult from pupae are variable in insects.
30. Insect emerged from hatching of egg can be a larva or nymph. All immature stages of holometabolous insects are called as larvae. Examples are butterflies, flies and beetles. True larvae are distinct from final adult stage while nymphs are more closely appear as adult.
31. Larvae in different orders of insects are known by different names. Larvae of butterflies and moths are called as caterpillars. Larvae of flies and beetles are called as maggots and grubs respectively. There are four types of larvae on basis of development of appendages. These are protopod, polypod, oligopod and apodous larvae.
32. Heteromorphosis is type of larval development which involves radical change in larval forms between successive larval instars. It is common in parasitic and predaceous insects, such as some wasps where change in habit occurs during development of larvae.
33. Pupa After completing larval growth and development through moulting at each instar, pupal stage is formed. Pupa is a resting and inactive stage of insects with holometabolous development. Moulting period of last stage larvae into pupae is called as pupation.

34. Generally three types of pupae are recognized according to presence or absence of functional mandibles which is used by adult to emerge from cocoon or pupal cell. These are exarate, obtect and coarctate pupae.
35. Following are the significances of pupa:
    - Acts as transitional phase
    - Diapausing stage
    - Protection during adverse condition
    - Time-limited ecological vulnerability
    - Defense mechanisms
    - Competition
    - Reconstruction of adult organs
36. Post-embryonic development is divided into a series of immature stages in which each stage is distinct from the next one through a moult. Thus anatomical and morphological change in forms of immature stages to form adult (or imago or imaginal) is known as metamorphosis. Process of metamorphosis varies with different insects. Therefore, it is necessary to understand various types, theories and importance of metamorphosis in insect life.
37. Heterometabola occurs in Exopterygote insects (have external wing growth), which pass through a simple metamorphosis. Thus it is direct or incomplete metamorphosis. A pupal stage is absent and immature insects are called as nymphs.
38. Holometabola occurs in Endopterygote insects (wings form internally), which pass through a complex metamorphosis. In this, the young are larvae and adult is preceded by a pupal instar. Hence, this is also known as indirect or complete metamorphosis.
39. The process of formation of organs of an imago from imaginal discs inside the pupa is known as histogenesis and it results in the formation of the imago.
40. These theories of metamorphosis revealed following facts:
    - Arthropod groups have monophyletic origin, i.e., they have evolved from a common ancestor.
    - Arthropods groups are diphyletic, i.e., two main subdivisions of groups evolved from common ancestor.
    - Each major group evolved autonomously of the other, i.e., groups have a polyphyletic origin.
41. Since metamorphosis evolved, it has played very important roles in insect's life for their success on this planet. Followings are important roles of metamorphosis:
    - Eliminate competition
    - Resource utilization and accumulation
    - Developmental size thresholds

NOTES

- Different pattern of life cycle
- Adult development
- Species diversification

42. Some hemimetabolous groups, such as thrips and some hemipterans, have independently evolved a holometabolous-like lifestyle. This particular life cycle with a quiescent stage in between nymph and adult stage is known as neometabolan.

4.9 SUMMARY

- Reproduction in most of the insect species is bisexual. Egg cell produced by female insect develops when fuse with the spermatozoa cell introduced by the male.
- Insect reproductive system comprises of paired sexual gonads that is the ovaries of female and testes of male.
- Male reproductive system consists of internal reproductive organs, spermatozoa and external reproductive organs.
- Male reproductive organs have paired testes (in butterfly these fuse to form a single median organ), paired vasa deferens and seminal vesicles, a median ejaculatory duct and various accessory glands.
- Testes usually lie either above or below gut in abdomen and are near to middle axis. Each testis has a series of testis tubes or testicular follicles. These vary in number and arrangement in different insects. Follicles can open into vas deferens.
- Number of testis tubes ranges from one in ground and aquatic beetles to more than 100 in grasshoppers.
- In some butterflies, the testicular follicles are not completely separated from each other.
- Testes of flies contain a simple and undivided sac that form single follicle.
- Distal zone is the germarium in which spermatogonia are produced from germ cells. A prominent apical cell is also present in grasshoppers, cockroaches, bugs and butterflies. Function of apical cell is to supply nutrients to spermatogonia.
- Vas deferens is a tube with a thick epithelium, a basement membrane and has a sheet of circular muscle externally.
- The epithelium of the ejaculatory duct is one cell thick. As it is epidermal in origin, it is lined with cuticle. Often at least a part of the wall is muscular. Parts of the wall of the duct may be glandular, contributing reproductive proteins to the ejaculate.
- Mayflies have no ejaculatory duct; instead vasa deferentia connect directly to paired genital openings.
- Earwigs have paired ejaculatory ducts whereas, one of the ducts becomes vestigial in some insect, such as European earwig.

- Ejaculatory duct in honeybee is entirely without muscles.
- Accessory glands in male are ectodermal or mesodermal in nature, hence are called as ectadenia or mesadenia, respectively.
- External parts of male reproductive system are collectively called as genitalia. Genitalia involved in coupling with the genitalia of female and introducing sperm into female body.
- Pair of primary phallic lobes is positioned in posterior ventral surface on ninth segment.
- Phallic lobes split to produce an internal pair of mesomeres and external parameres. Mesomeres and parameres are collectively called as phallomeres.
- Mature spermatozoa in most insects are flagellate containing head and tail parts. The insect sperm exhibit high variation in morphology.
- Flagellate spermatozoa have a characteristic cell membrane that is about 10 nm thick. Cell membrane is covered on exterior by coating of glycoprotein called as glycocalyx.
- Larger area of head part is filled by nucleus.
- Process of conversion from primitive germ cell spermatogonium into mature germ cell spermatozoa is called as spermatogenesis.
- Spermatogonia are the cells that mitotically divide to give rise spermatocytes. It occurs in zone of growth testicular follicle.
- Female reproductive system contains a pair of ovaries that are joined with a pair of lateral oviducts. These are fuse to lead as a median oviduct that opens posteriorly into a genital cavity. Spermatheca for storing sperm situated at the opening from the genital cavity.
- Paired ovaries situated above or lateral to the gut in abdomen. Each ovary has many egg-tubes called ovarioles similar with testicular follicles of testis in male.
- The oocytes grow and mature in ovarioles. An ovariole is formed distally into a long terminal filament having cellular core lined by tunica propria. Typically each filament from each ovary pooled to produce a suspensory ligament. Ligaments of both sides unite into a center ligament.
- Number of ovarioles in an ovary varies according to body size, life histories and taxonomic position of insect species. Basically, larger size of species has more number of ovarioles than small size insect.
- A typical ovariole is an extended tube that contains the developing eggs arranged in a single chain. Wall of an ovariole is a delicate transparent membrane made up of two layers.
- An inner coat is a layer of epithelium called as tunica propria whose cells rest upon a basement membrane.
- An outer layer called tunica externa is a peritoneal sheath of connective tissue. External sheath has non-penetrating tracheoles.
- Meroistic is advanced kind of ovariole. In this, materials required for development of oocyte is provided by nurse cells or trophocytes whose genomes is increased through endomitosis.

NOTES

- Usually single spermatheca is found in most female insects. It is used for storage of sperm that are received from male during copulation. Later these stored sperm are utilized for fertilization of eggs.
- Protoplasm of mature egg has plentiful yolk also called vitellus. Yolk nourishes the developing embryo. Yolk consists of globules of fat and protein that mostly cover the nucleus or germinal vesicle.
- Chorion is perforated by microscopic pores called as aeropyles. These allow respiratory exchange of oxygen and carbon dioxide with little loss of water.
- Micropyle is opening near anterior end of chorion. It serves as a passage for entry of sperm during fertilization.
- Process for production of eggs or ova in female's body is called as oogenesis.
- Seminal vesicles are two groups of numerous small glistening white sacs. It present on ventral surface of anterior part of ejaculatory duct. It serves to store sperms.
- Most insects reproduce sexually and also are dioecious that is male and female insects are separate. Sexual reproduction involves several physiological events, such as mating of insects and sperm transfer, egg (oocyte) development and egg fertilization.
- Mating behaviour of most insects can be subdivided into four parts. These parts are i. Location and recognition of a mate, ii. Courtship, iii. Pairing and iv. Copulation.
- Main function of mating behaviour is to ensure the transfer of sperm from male to female.
- Pheromones are most common signal used by insects in mate location. Volatile chemical attractants are both highly specific and capable of exerting their effect over a long distance.
- Pheromones are produced by females and are used by both diurnal and nocturnal insects.
- Copulation is the reproductive or mating act in which male reproductive organ, enters female reproductive organ.
- In mosquitoes, copulation completes within few seconds, whereas seed bugs remain coupled for five hours, for 8–10 hours in locusts and for up to 60 hours in tree locusts.
- Duration of coupling after insemination (sperm transfer) depends on male density in population. In green stink bug, copulation continues for 1-2 days if the population contain majority of females. While, this become prolonged for up to seven days when majority of males are present.
- Process of sperm transfer by male to female reproductive organs during copulation is called as insemination.
- Sperm transfer involves lubrication that is provided by seminal fluids and spermatophore formed in some insects. Secretions of male reproductive

tract perform these functions. Secretions are involved with final maturation of sperm in female.

- Copulation initiates oocyte development, oviposition and sometimes inhibition of sexual receptivity in female. It occurs through enzymes or peptides passed to female reproductive system from secretions of male accessory gland.
- Pre-vitellogenesis is a process where there is an increase in nuclear and cytoplasmic material in oocyte with no addition of yolk.
- Vitellogenesis is a process of synthesis and deposition of large amount of yolk in oocyte.
- Yolk is also called as deutoplasm, is nutrient-bearing portion of egg and supply food to embryo at the earliest stages of development.
- Oocyte near to oviduct in each ovariole is called as terminal oocyte.
- Fat body made up of storage cells and distributed throughout haemocoel (body cavity) near to epidermis, digestive organs and ovaries.
- *Lipophorin* is the major haemolymph protein responsible for lipid transport between tissues of insects.
- Female sperm storage is a process in which sperm transferred to a female during mating are temporarily retained within a specific part of reproductive tract before oocyte or egg, is fertilized.
- Females of many insects store sperm in spermatheca after she get sperm from one or more males during copulation.
- Sexually mature male and female cockroaches usually mate during night from March to September.
- Most insect species are bisexual and females lay eggs that have large amount of yolk. Such insects are called oviparous.
- In viviparity, female insect keep their fertilized eggs inside their genital tract until they develop into young ones and then these are laid.
- Eggs of some female insect species undergo development without fertilization of their eggs. This mode of asexual reproduction is called as parthenogenesis.
- Parthenogenesis is divided into two broad forms namely: Thelytoky and Arrhenotoky.
- In thelytoky, all unfertilized eggs develop to form diploid females. This is also called diploid parthenogenesis.
- In arrhenotoky, unfertilized haploid eggs grow into males and fertilized diploid eggs grow into females.
- After mating and sperm transfer in insects, fertilization of ova takes place in female insects that eventually initiates embryonic development in fertilized egg called zygote.
- Events before fertilization involves ovulation, monospermy, polyspermy and sperm utilization.

- Events during fertilization involves sperm capacitation, sperm entry to egg, sperm penetration, egg activation and amphimixis.
- Events after fertilization involves oviposition, embryonic development and egg hatch.
- An egg gets fertilized when it moves into common oviduct and genital cavity where a few sperm are released from the spermatheca. This event of egg release is called as ovulation.
- Ovulation is the movement of an egg from the ovary into the lateral oviduct. This also provides stimulus to maturation of oocytes.
- Several spermatozoa enter egg. Only one of these is usually utilized in fertilization of egg. This called as monospermy.
- Polyspermy is the entry of two or more sperm into an egg and is common in insects.
- After fertilization of eggs in female body, fertilized egg deposited, and then embryonic development begins with first mitotic division of zygote nucleus and terminates at hatching.
- After fertilization of eggs in female body, eggs are deposited outside environment by oviparous insects. This process is called oviposition.
- In many animals, early cleavage is division of both cytoplasmic and nuclear material to form cells known as blastomeres. This type of cleavage is called as total or complete cleavage.
- Most of energids move to surface of egg to form the blastoderm. But some energids remains in yolk to form yolk cells that is called as vitellophages.
- Gastrulation is process of invagination and proliferation of cells along midline in egg.
- After embryonic development and egg hatch, neonates or immature stages of insects are come out. These neonates are known as larvae in case of holometabolous insects.
- Development process of larvae and pupae is also called as postembryonic development.
- Insect emerged from hatching of egg can be a larva or nymph. All immature stages of holometabolous insects are called as larvae.
- Larvae in different orders of insects are known by different names. Larvae of butterflies and moths are called as caterpillars. Larvae of flies and beetles are called as maggots and grubs respectively.
- There are four types of larvae on basis of development of appendages. These are protopod, polypod, oligopod and apodous larvae.
- In protopod larva, larvae come out from eggs which have very less amount of yolk and this occurs during early stages of embryonic development.
- Oligopod larva is the least modified form of larvae relating to adult morphology. Oligopod larva is hexapodous with a well-built head capsule and mouthparts as similar to those of adult. This type of larva has no compound eyes.

- The apodous larvae have no legs and poorly sclerotized cuticle. Apodous larvae have no true legs and are worm-like or maggot-like in appearance. They dwell in soil, mud, dung, decaying animal, plant matter and inside bodies of other organisms in form of parasites or parasitoids.
- Heteromorphosis is type of larval development which involves radical change in larval forms between successive larval instars.
- During developmental stages, larvae consume more food to fuel up their transition into adult form.
- Advantages of larvae include the avoidance of competition for resources with adults and thus reduction of mortality of insects. Diets and life pattern larvae are quite different from those of their adults.
- After completing larval growth and development through moulting at each instar, pupal stage is formed.
- Pupa is a resting and inactive stage of insects with holometabolous development.
- Moulting period of last stage larvae into pupae is called as pupation.
- At end of pupal period, it is look like a fully developed adult within cuticle of pupa called as a pharate (covered) adult.
- In exarate or free pupa, the appendages, such as the wings and legs extend freely from body.
- When pupae have articulated mandibles are known as decticous pupae. Another type of pupae has immobile mandibles is called as adecticous.
- In obtect pupa appendages, such as wings and legs are firmly glued down to body by moulting fluid secreted after final larval ecdysis.
- In some dipteran flies, such as botfly, skin of last instar larva is retained so as to cover pupa and become hardened. It completely separated from insect which it surrounds. This type of pupal casing or capsule is called as a puparium and pupa protected in this manner are called as coarctate.
- An immobile pupa is susceptible to attack by predators or parasites and to changes in climatic conditions. As pupal stadium last for a large time, thus to obtain protection against such adversities pupa has a thick, tanned cuticle.
- Pupae are immobile stages that face a number of challenges, including predation and infection. Pupae have evolved different anti-predator defense mechanisms, such as crypsis.
- A small number of insects have unprotected pupae that are suspended from a silk pad. This type protection of pupa is found in some butterflies, such as monarch butterflies.
- Evagination is a process of turning outward, it takes place due to a reordering of cells in imaginal disc and by the same time, it tends to rise in surface area.
- Post-embryonic development is divided into a series of immature stages in which each stage is distinct from the next one through a moult. Thus anatomical and morphological change in forms of immature stages to form

adult (or imago or imaginal) is known as metamorphosis. Process of metamorphosis varies with different insects.

- Metamorphosis is divided into two main groups: heterometabola and holometabola.
- Heterometabola occurs in Exopterygote insects (have external wing growth), which pass through a simple metamorphosis.
- Holometabola occurs in Endopterygote insects (wings form internally), which pass through a complex metamorphosis. In this, the young are larvae and adult is preceded by a pupal instar. Hence, this is also known as indirect or complete metamorphosis.
- The building of new structures is brought about by growth centres called imaginal buds or discs.
- The process of formation of organs of an imago from imaginal discs inside the pupa is known as histogenesis and it results in the formation of the imago.
- The prothoracic glands are a pair of small glands in the first thoracic segment, they produce a hormone called ecdyson which brings about moulting and development of imaginal discs and reproductive organs.
- Ametaboly is the basic and most primitive pattern of insect development in which there is no metamorphosis.
- Paurometaboly is the type of development, which occurs in less primitive insects like cockroaches, grasshoppers, praying mantis and white ants.
- Complete metamorphosis is a kind of morphological change during post-embryonic transformation in which larva has no similarity with adult and there is always a pupal stage.
- Complete metamorphosis takes place in beetles (Coleoptera), flies (Diptera), wasps (Hymenoptera) and butterflies and moths (Lepidoptera). In holometabolous insects, transition from larva to adult takes place through non-feeding, transitional stage known as pupa.
- Brood is defined as whole pre-imaginal period (eggs, larvae and pupae). Egg and early larval stages live in uncapped brood cells. Last two days of larval stage, pupal stage and first half-day of adult stage occur under capped brood cells.
- Scientists have studied that arthropods with various life histories (cycles) evolved from their ancestors.
- Arthropod groups have monophyletic origin, i.e., they have evolved from a common ancestor.
- Arthropods groups are diphyletic, i.e., two main subdivisions of groups evolved from common ancestor.
- Main advantage of complete metamorphosis is eliminating competition between the young and old. Larvae and adults occupy very different ecological niches.

- The main difference between complete metamorphosis and incomplete metamorphosis is that complete metamorphosis has a very active, voraciously feeding larva and an inactive and non-feeding pupa whereas incomplete metamorphosis has nymph, which resembles a miniature adult.
- Adaptations of the larval and adult stages were developmentally uncoupled. This allowed evolution of a larval stage with reduced mobility but enhanced capacity to exploit food resources without affecting adult specializations for dispersal and reproduction.

4.10 KEY TERMS

- **Spermatogenesis:** Process of conversion from primitive germ cell spermatogonium into mature germ cell spermatozoa is called as spermatogenesis.
- **Oogenesis:** Process for production of eggs or ova in female's body is called as oogenesis.
- **Copulation:** Copulation is the reproductive or mating act in which male reproductive organ, enters female reproductive organ.
- **Insemination:** Process of sperm transfer by male to female reproductive organs during copulation is called as insemination.
- **Micropyle:** Micropyle are funnel-shaped pores usually located near the anterior pole of the egg. This pore allow the entry of sperm when the egg is fertilized.
- **Vitellogenesis:** Vitellogenesis is a process of synthesis and deposition of large amount of yolk in oocyte.
- **Polyembryony:** Polyembryony is the mode of reproduction that involves formation of two or more embryos from a single egg.
- **Yolk:** Yolk is also called as deutoplasm, is nutrient-bearing portion of egg and supply food to embryo at the earliest stages of development.
- **Terminal oocyte:** Oocyte near to oviduct in each ovariole is called as terminal oocyte.
- **Fat Body:** Fat body made up of storage cells and distributed throughout haemocoel (body cavity) near to epidermis, digestive organs and ovaries.
- **Lipophorin:** Lipophorin is the major haemolymph protein responsible for lipid transport between tissues of insects.
- **Parthenogenesis:** Eggs of some female insect species undergo development without fertilization of their eggs, this mode of asexual reproduction is called as parthenogenesis.
- **Monospermy:** Several spermatozoa enter egg. Only one of these is usually utilized in fertilization of egg called as monospermy.
- **Polyspermy:** Polyspermy is the entry of two or more sperm into an egg and is common in insects.

- **Ovulation:** Ovulation is the movement of an egg from the ovary into the lateral oviduct.
- **Oviposition:** After fertilization of eggs in female body, eggs are deposited outside environment by oviparous insects, this process is called as oviposition.
- **Gastrulation:** Gastrulation is process of invagination and proliferation of cells along midline in egg.
- **Postembryonic development:** Development process of larvae and pupae is also called as postembryonic development.
- **Metamorphosis:** Metamorphosis is the process of transformation of an immature larval stage into adult or imaginal stage which is sexually mature.
- **Heteromorphosis:** Heteromorphosis is type of larval development which involves radical change in larval forms between successive larval instars.
- **Pupa:** Pupa is a resting and inactive stage of insects with holometabolous development.
- **Pupation:** Moulting period of last stage larvae into pupae is called as pupation.
- **Decticous pupae:** When pupae have articulated mandibles are known as decticous pupae.
- **Evagination:** Evagination is a process of turning outward, it takes place due to a reordering of cells in imaginal disc and by the same time, it tends to rise in surface area.
- **Histogenesis:** The process of formation of organs of an imago from imaginal discs inside the pupa is known as histogenesis and it results in the formation of the imago.
- **Brood:** Brood is defined as whole pre-imaginal period, i.e., eggs, larvae and pupae.

4.11 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. What are the internal reproductive organs in male insects?
2. Give the functions of accessory glands.
3. Define the following terms:
   i. Vitellarium
   ii. Meroistic ovariole
   iii. Haemocoelic insemination
   iv. Pedogenesis
   v. Polyspermy

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vi. Germ anlage
vii. Heteromorphosis
viii. Syncytial cleavage
ix. Metamorphosis
x. Spermatheca
xi. Spermatophore

4. What are the different types of mating seen in insects?
5. Write a short note on courtship in insect.
6. How is polymorula formed?
7. What are the different ways in which sperm is transferred by male to female reproductive organs during copulation?
8. How does sperm transfer occur without spermatophore?
9. Write about the functional significance of haemocoelic insemination.
10. Give a short note on vitellogenesis and its types.
11. What is the composition of yolk and how is it formed?
12. Distinguish between polyembryony and parthenogenesis.
13. Give a brief note on polyembryony in parasitic encyrtidae wasps.
14. What are the types of parthenogenesis?
15. Give advantages and disadvantages of parthenogenesis.
16. How does fertilization in insects occur?
17. How is sex determination done in insects?
18. Write about gastrulation and the events that take place during gastrulation.
19. What are energids?
20. Write in short about organogenesis and its types.
21. How many types of larvae are there? Write in short about them.
22. Distinguish between first and second form of heteromorphosis.
23. Write a brief note on growth of larvae.
24. What do you understand by obtect pupa?
25. What are different means of pupal protection?
26. Give the significance of pupa.
27. What are the different types of movement seen in pupa?
28. What do you understand by imaginal disc?
29. What is endopterygote?
30. How is paurometaboly different from holometabolous?
31. Brief a note on holometaboly in honey bee.
32. Write about monophyletic and diphyletic theories of metamorphosis.

Long-Answer Questions

1. Discuss about reproductive organs in insect.
2. Distinguish between internal and external organ of male reproductive system in insects.
3. Elaborate a note on male reproductive organs and their modifications.
4. Illustrate with the help the diagram development and basic features of male genitalia.
5. Write a descriptive note on female reproductive organs.
6. Describe different types of ovarioles in different insect species.
7. Draw a well-labelled diagram to show the difference between different types of ovarioles in insects.
8. Explain the difference between male and female reproductive organs with the help of table.
9. Write a descriptive note on physiology of reproduction.
10. What are the different mating behaviours possessed by insects?
11. Explain the process of sperm transfer by male to female reproductive organs during copulation in various insects.
12. Describe in detail about the functions, composition, formation and role of yolk.
13. Explain the process of reproduction in cockroach with the help of well-labelled diagram.
14. Write a detailed note on polyembryony.
15. Discuss about parthenogenesis in detail.
16. Explain the events that occur before fertilization.
17. Draw a chart to show the sequence of events that occur during embryonic development in insect egg.
18. Discuss about the events that occur after fertilization.
19. Explain about gastrulation and events take place during gastrulation in detail.
20. Describe various types of larva and their significance.
21. Discuss about pupa, its types, significance and its protection and development in detail.
22. Write a descriptive note on metamorphosis and its types in insect.
23. Discuss about different theories of metamorphosis.
24. Explain the importance of metamorphosis.

4.12 FURTHER READINGS

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