

Chapter 2

Structure and Function



This chapter introduces the basics of anatomy and physiology of insects that are necessary for the classification of insects and development of successful pest control strategies. An understanding of external structures of insects is a prerequisite for their taxonomy and identification. Fundamental life processes such as sensing, reproduction and locomotion are outlined for the comprehension of insect behaviour, population dynamics and dispersal.

major **tagmata** or body parts, **head**, **thorax** and **abdomen**, as summarised below. The body parts, their appendages and respective functions are further discussed in this chapter.

Body Part	Main Function	No. of Segments
Head:	feeding, sensing and nervous coordination	6
Thorax:	locomotion (legs, wings)	3
Abdomen:	digestion, reproduction and excretion	11 or fewer

2.1 External Anatomy

Insects show great diversity of shape and form. A **generalised model** as shown in **fig. 2-1** is therefore used to study structure and function. **Comparative anatomy** studies adaptations of basic structures like legs or mouthparts to various ways of feeding or locomotion. Despite the diversity of shapes and forms, most structures are built according to the same plan and are then called **homologous**. **Fig. 2-2** indicates **orientation** and **anatomical planes** that describe the location of various body parts. Adult insects are generally made up of three

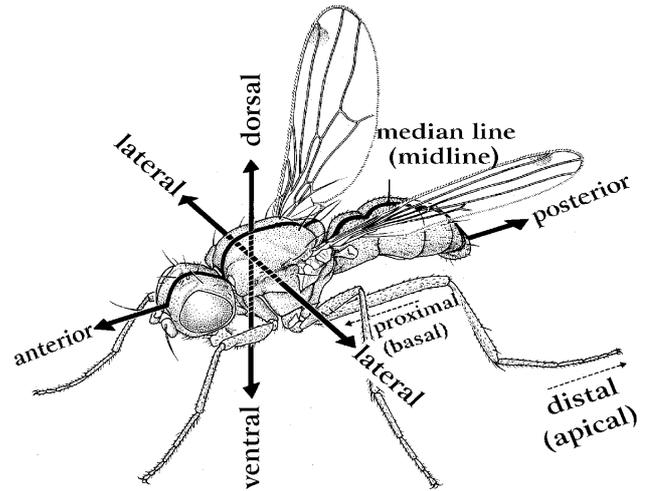


Fig. 2-2: Orientation and anatomical planes (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

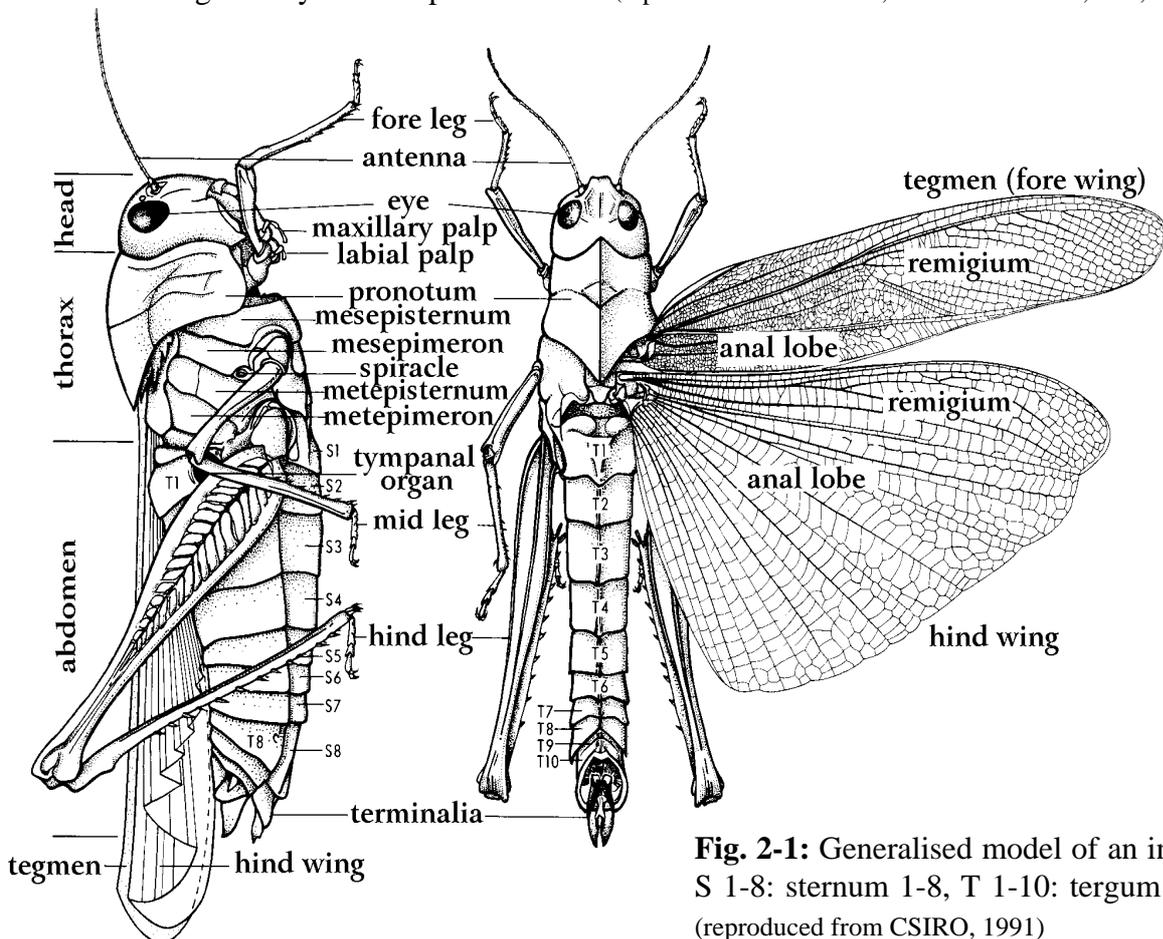


Fig. 2-1: Generalised model of an insect. S 1-8: sternum 1-8, T 1-10: tergum 1-10 (reproduced from CSIRO, 1991)

2.1.1 Integument and Exoskeleton

The **integument** is the outer protective covering of insects and other Arthropoda, forming the **exoskeleton** or body wall. Unlike vertebrates that have an internal skeleton (endoskeleton), insects possess a capsule-like exoskeleton. The exoskeleton provides support for soft tissues, attachment for muscles, protection against physical stress like mechanical impact and evaporation, protection against germs and other parasites. Moreover, the exoskeleton bears sense organs. The integument is composed of the basement, the epidermis and the **inert** (dead) cuticle as shown in **fig. 2-3**. The cuticle consists of structural proteins, pigments and **chitin**. Chitin is a tough and rigid protein that undergoes a tanning process directly after the moult. Thus the initially soft cuticle hardens or sclerotizes. Once hardened, the cuticle is inflexible and can not grow any more. Therefore the growth of an insect is restricted and makes **moult**s necessary for gaining body size, as described in **chapter 2.2.9**. The outmost layer of the cuticle is wax-covered and sometimes has an additional cement layer.

The exoskeleton is composed of various plates joined together with softer connecting membranes, thus allowing movement especially in the regions of the joints as shown in **figs. 2-18** and **2-22**.

The body coloration of insects is either made from **physical** or **pigmentary colours**. Physical colours like the iridescent metallic colours of beetles and butterflies are due to the phenomenon of interference. Pigmentary colours like the green colour of grasshoppers are the result of conjugated double bonds of pigments in the cuticle. The latter are not persistent and fade away, for instance the greenish-yellow colour of a grasshopper turns into brown, after the animal dies and its body dries.

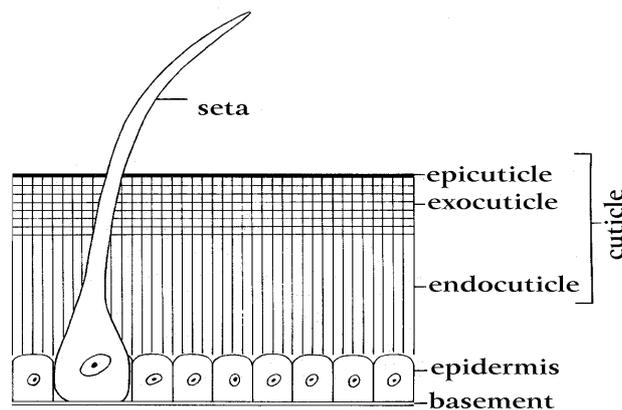


Fig. 2-3: General structure of the insect cuticle (reproduced from Coulson, R.N. and Witter, J.A., 1984)

2.1.2 Head

The head (**cranium** or **caput**), is the anterior capsule-like structure that bears the brain, mouthparts and sense organs like antennae and eyes. The insect head consists of six fused segments, the **labral** segment, the **antennal** segment, the **postantennal** segment, the **mandibular** segment, the **maxillary** segment and the **labial** segment. The shape of the head varies considerably in relation to how the insect feeds. Insects with chewing mouthparts normally have large heavy heads that are directed downward or forward, whereas insects with piercing-sucking mouthparts have small heads that are quite variable in appearance and position. The generalised view of the head is shown in **figs. 2-4** and **2-6**.

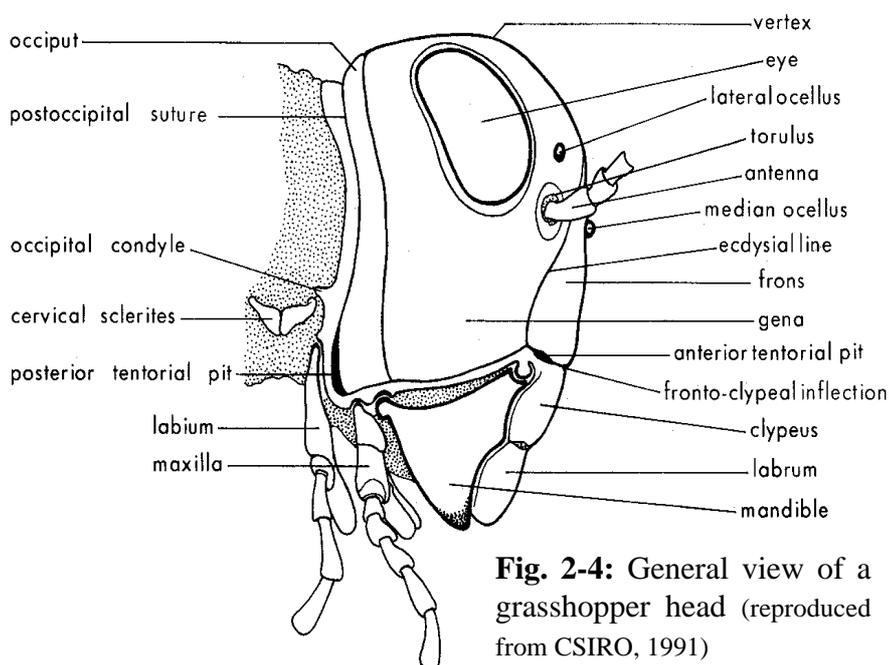


Fig. 2-4: General view of a grasshopper head (reproduced from CSIRO, 1991)

2.1.2.1 Antennae

The antennae or feelers are a pair of mobile, segmented appendages located on the anterior portion of the head between the compound eyes. The antennae are part of the antennal segment (segment 2) and are homologous to the true legs of the thorax. All insects except Protora possess one pair of antennae. The primary function of the antennae is sensory. Various types of small hairs (**sensilla**) located on the antennae act as mechano- (tactile), chemo-, hydra-, sound, and temperature receptors. Antennae play an important role in the mating process of many insects. Feelers are sometimes greatly enlarged in males to increase the surface area and consequently the efficiency of the sense of smell. Antennae are commonly used as a taxonomic characteristic in identifying insects because of the distinctive variations in size and shape shown in **fig. 2-5**.

2.1.2.2 Mouthparts

A basic understanding of the different types of mouthparts is important because feeding traces and type of damage often tell to which order the insect that has caused the particular damage belongs. It is also important to recognise

mouthpart types since they vary considerably and are always used in classifying insects. Mouthparts are generally divided into two major types, **mandibulate** or **chewing** and **piercing-sucking**. All types of mouthparts have evolved from chewing mouthparts as adaptations to different sources of food. The biting mandibles of a cockroach for instance are **homologous** to particular parts of a bug's proboscis, even though the latter is used for piercing its plant or animal host. The mandibles of these two different mouthparts have evolved from the same ancestral structure but have different functions.

Mouthparts are composed of several components, as shown in **figs. 2-6 to 2-17**. The five basic parts are

- **the labrum**, a movable flap attached to the front part of the head, covering the mouth like the upper lip
- **the mandibles**, a paired appendage of head segment 4, typically hard and sclerotized with various sets of teeth (**endites**) or brushes used like jaws
- **the maxillae**, a paired appendage of head segment 5, consisting of several parts and used for tasting and uptake of food

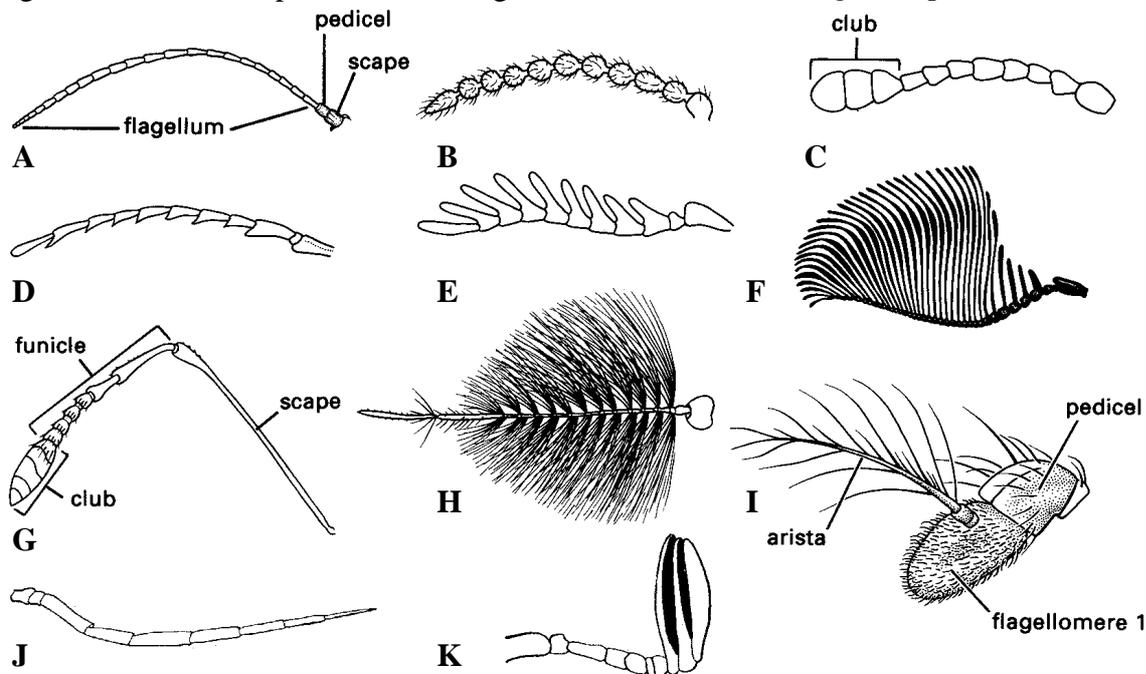


Fig. 2-5: Types of antennae (A) filiform (thread-like), (B) moniliform (bead-like), (C) clavate or capitata (clubbed), (D) serrate (saw-like), (E) pectinate (comb-like), (F) flabellate (fan-shaped), (G) geniculate (elbowed), (H) plumose (with whorls of setae), (I) aristate, (J⁺) setaceous (tapering), (K⁺) lamellate (leaf-like) (reproduced from Gullan, P.J. and Cranston, P.S., 1994; Ross, H.H. et al., 1982⁺)

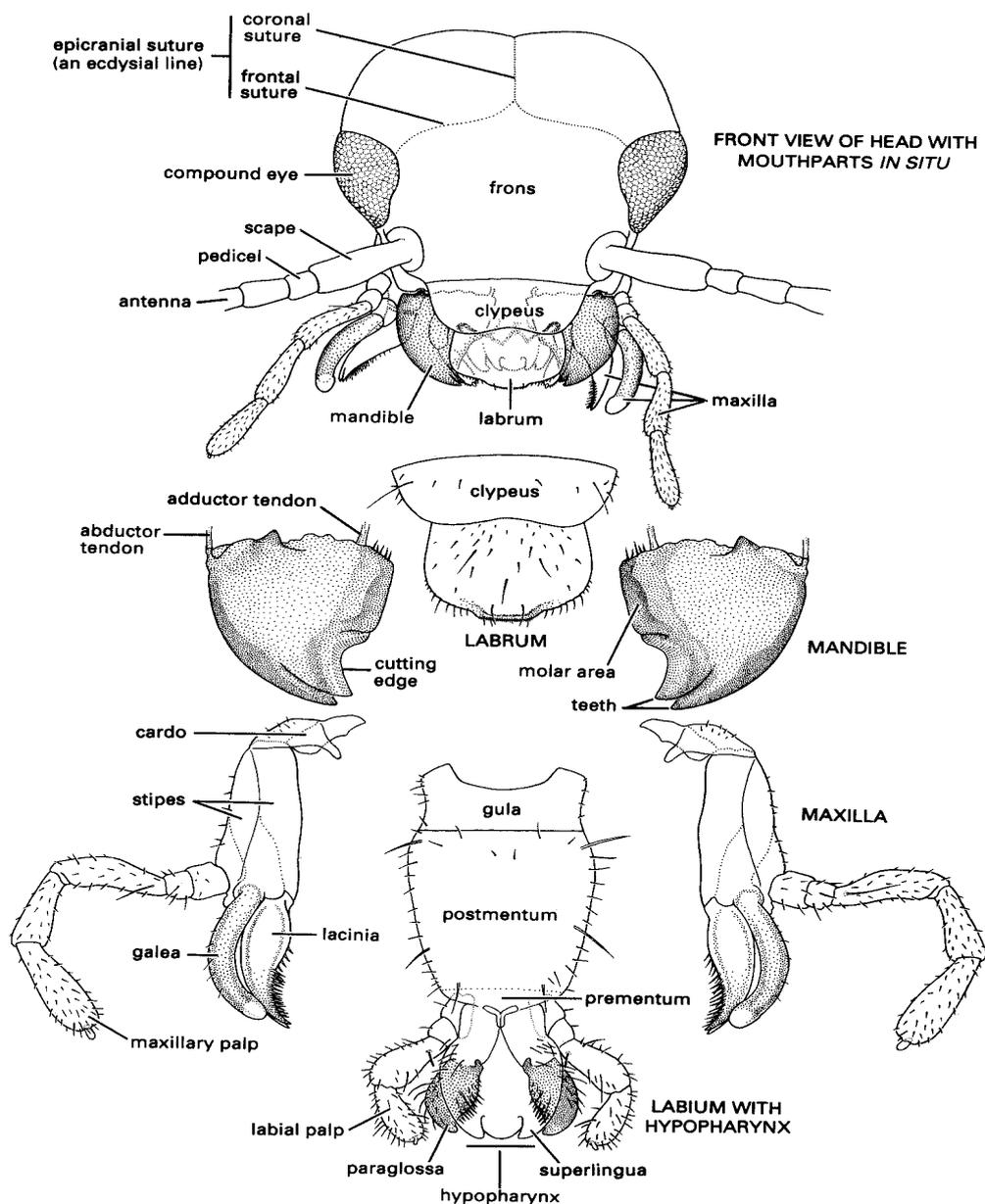


Fig. 2-6: Components of the mouthparts of an earwig (Dermaptera). Frontal view of head at top and dissected mouthparts at bottom (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

- **the hypopharynx**, an unpaired, tongue-like organ
- **the labium**, a paired appendage of segment 6, forming the lower lip. The labium is also referred to as a fused pair of second maxillae, consisting of various parts. The function is similar to the first pair of maxillae.

Chewing Mouthparts

This type, shown in **figs. 2-4, 2-6** and **2-7** generally occurs in primitive insect orders like silverfish (**Thysanura**), crickets, locusts and grasshoppers (**Orthoptera**) and cockroaches

(**Blattodea**). Chewing mouthparts are also found in larval instars of higher developed orders like beetles (**Coleoptera**), moths and butterflies (**Lepidoptera**), true flies (**Diptera**), ants, wasps and bees (**Hymenoptera**) and in adults of **Coleoptera**, **Hymenoptera** and other orders. The mandibles might be reduced as in weevils (see **fig. 5-38**), so that the mouthparts can be confused with a piercing-sucking proboscis. Chewing mouthparts are easily recognised by a large head that bears the muscles operating the heavy sclerotized mandibles. Insects with chewing mouthparts bite and chew their food.



Fig. 2-7: Chewing mouthparts of a Mecoptera larva (reproduced from Ross, H.H. et al., 1982)

Filtering type

The filtering type of mouthparts, as shown in **fig. 2-8**, can be found in some aquatic insects and is derived from mandibulate mouthparts.



A



B

Fig. 2-8: Filtering mouthparts of the black fly (A) *Crozetia sp.*, (B) *Simulium sp.* (Simuliidae) (reproduced from Ross, H.H. et al., 1982)

Cutting-sponging type

This type, shown in **fig. 2-9**, can be found in horse flies and some other Diptera. The sharp mandibles are for cutting the integument of a mammal host, causing blood to flow from the wound. The blood is then collected by a sponge-like development of the labium and sucked into the mouth.

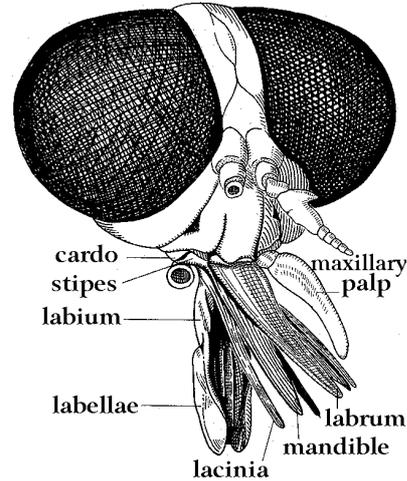


Fig. 2-9: Cutting sponging mouthparts of a horse fly (Tabanidae) (reprod. from Seifert, G., 1995)

Chewing-lapping type

The chewing-lapping type of mouthparts, as shown in **fig. 2-10** can be found in bees and wasps (Hymenoptera). Mandibles and labrum are of the chewing type for grasping prey, maxillae and labium are channelled to probe deep into the nectaries of blossoms.

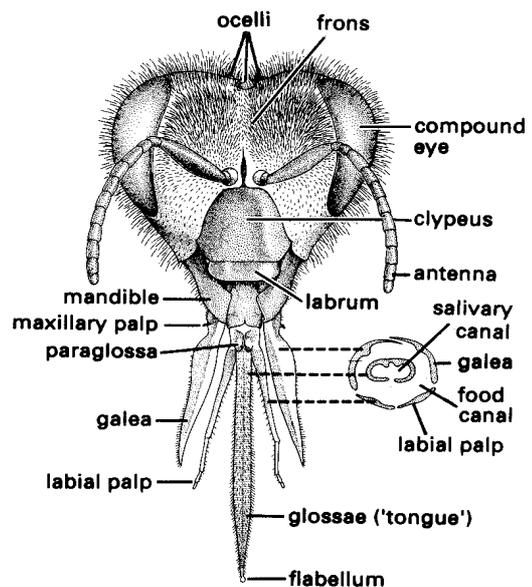


Fig. 2-10: Chewing-lapping mouthparts of the honey bee *Apis mellifera* (Apidae) (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

Piercing-sucking mouthparts

As shown in **figs. 2-11 to 2-14** this type usually appears as a rod-like beak, called a **proboscis** and is adapted for piercing plant or animal tissues and sucking sap or body juices. Insects with piercing-sucking mouthparts are found in orders such as **Hemiptera** (aphids, scale insects, cicadas, true bugs, etc.), **Siphonaptera** (fleas), some **Diptera** like mosquitoes and some **Phthiraptera** (lice). Labrum, mandibles and maxillae are slender and long and fit together to form a hollow needle. The labium forms a sheath to hold the needle rigidly. Mosquitoes inject pain killers and anti-coagulants prior to sucking.

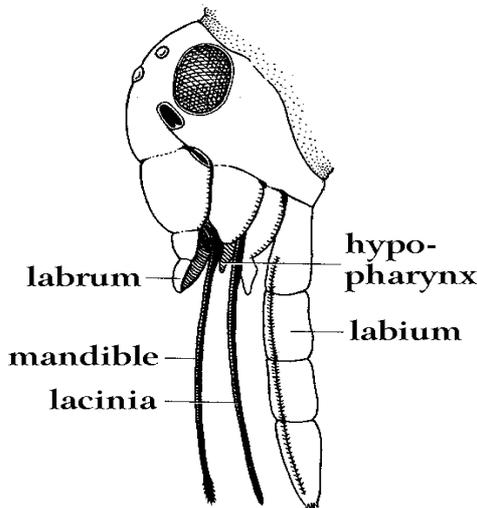


Fig. 2-11: Piercing-sucking mouthparts of a true bug (reproduced from Seifert, G., 1995)

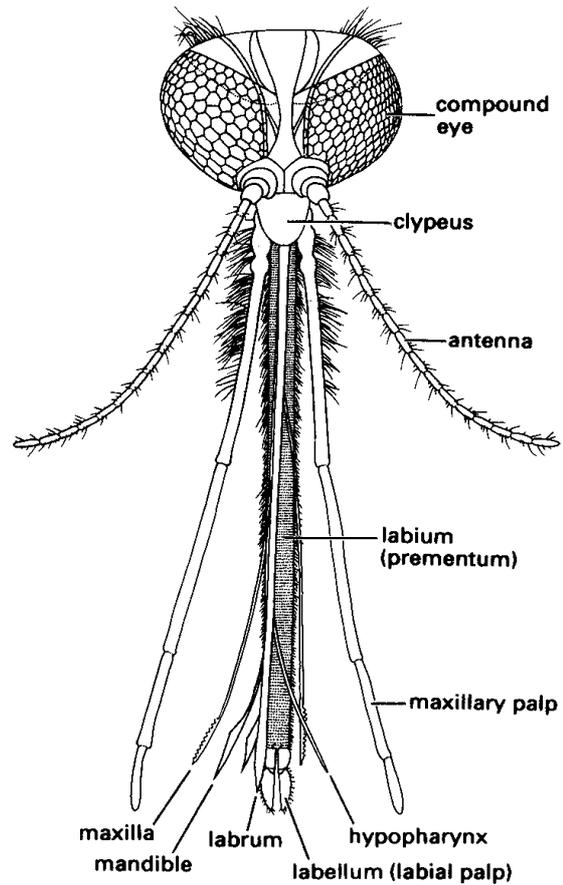
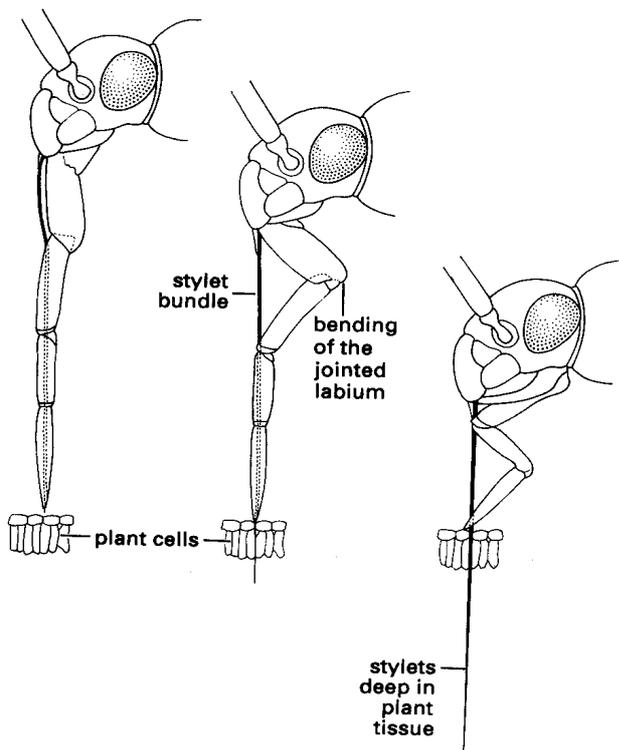


Fig. 2-12: Piercing-sucking mouthparts of a mosquito (reprod. f. Gullan, P.J. & Cranston, P.S., 1994)



Fig. 2-13: Piercing-sucking mouthparts of a first larval instar of the plant hopper *Macrosteles* spp. (reproduced from Ross, H.H. et al., 1982)

Fig. 2-14 (left): A phytophagous Hemiptera feeding with piercing-sucking mouthparts (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

Sponging mouthparts

Sponging mouthparts as shown in **figs. 2-15** and **2-16** are fitted for using either liquid or food soluble in saliva and can be found in many non-biting flies. This type is similar to the cutting-sponging type but the parts for chewing are non-functional. The apex of the proboscis called the **labella**, extrudes saliva and draws up the dissolved or pre-digested food into the mouth.

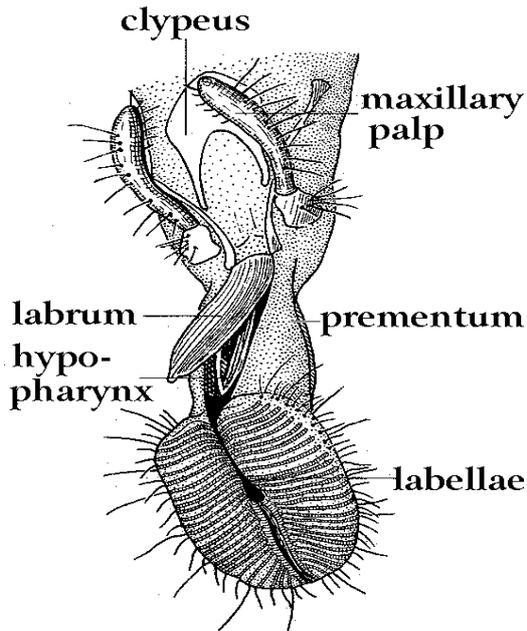


Fig. 2-15: Sponging mouthparts of the house fly *Musca domestica* (Muscidae) (reproduced with permission from Seifert, G., 1995)



Fig. 2-16: Sponging mouthparts of the vinegar fly *Drosophila melanogaster* (Drosophilidae) (reproduced from Ross, H.H. et al., 1982)

Siphoning-tube type

Mouthparts of the siphoning-tube type, as shown in **fig. 2-17**, are found in adult moths and butterflies (Lepidoptera). These insects suck nectar and other liquid foods by means of a long **proboscis**. The proboscis is composed only of united parts of the maxillae, forming a tube that opens into the oesophagus. The proboscis is coiled when not in use and stretched out, when the animal is drinking.

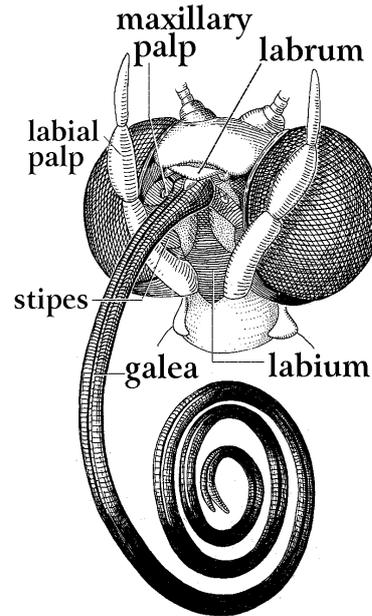


Fig. 2-17: Siphoning-tube type mouthparts of a butterfly (Lepidoptera) (reprod. from Seifert, G., 1995)

2.1.3 Thorax

The thorax is the middle body region of an insect, usually composed of three segments, the **prothorax**, **mesothorax** and **metathorax** as shown in **fig. 2-1**. The modified last thoracic segment of apocritan Hymenoptera is shown in **fig. 5-59**. The main function of the thorax is locomotion. Each segment bears one pair of legs. Winged insects (**Pterygota**) have one pair of wings attached to the second segment (mesothorax) and a second pair attached to the third segment (metathorax). All segments have an internal skeleton for the attachment of muscles. In grasshoppers (Orthoptera) and beetles (Coleoptera) the prothorax has a shield-like structure called the **pronotum**. The plates that make up the thorax, shown in **fig. 2-18**, are often of importance for the identification of an insect.

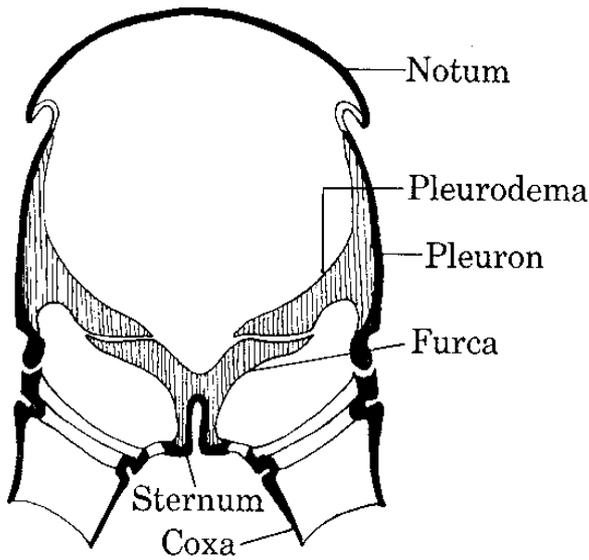


Fig. 2-18: Cross section of a thoracic segment (reproduced from Ross, H.H. et al., 1982)

2.1.3.1 Legs

The walking leg is the generalised leg from which all other types have evolved. It consists of **coxa**, **trochanter**, **femur**, **tibia**, **tarsus** and several **pretarsi**, as shown in **figs. 2-19, 2-20** and **2-31**. Insect legs are adapted for walking (**gressorial**), running (**cursorial**), jumping (**saltatorial**), clasping, grasping (**prehensile** or **raptorial**), holding, swimming (**natatorial**), and digging (**fossorial**) as can be seen from **fig. 2-20**. Even though all these legs look different and are used for different purposes, they are **homologous**, because they have evolved from the same ancestral origin and are made up of the same parts. Apart from thoracic or **true** legs, some caterpillars possess **false** abdominal

legs that are not homologous but **analogous** structures. Leg characteristics are often used in insect identification owing to the great variations in leg size, shape, number of tarsal segments (**tarsal formula**, **tarsomeres**), the number, shape and location of spines.

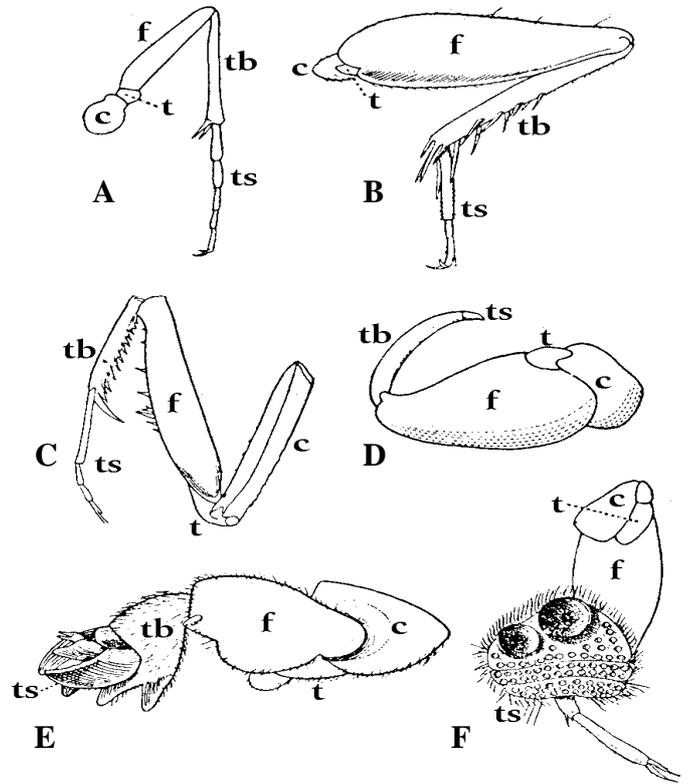


Fig. 2-20: Types of insect legs: (A) walking or running leg, (B) jumping hindleg of a grasshopper, (C) grasping foreleg of a praying mantid, (D) clasping foreleg of a bug, (E) digging foreleg of a mole cricket, (F) holding leg of an aquatic beetle; (c) coxa, (t) trochanter, (f) femur, (tb) tibia, (ts) tarsus (reproduced from Ross, H.H. et al., 1982)

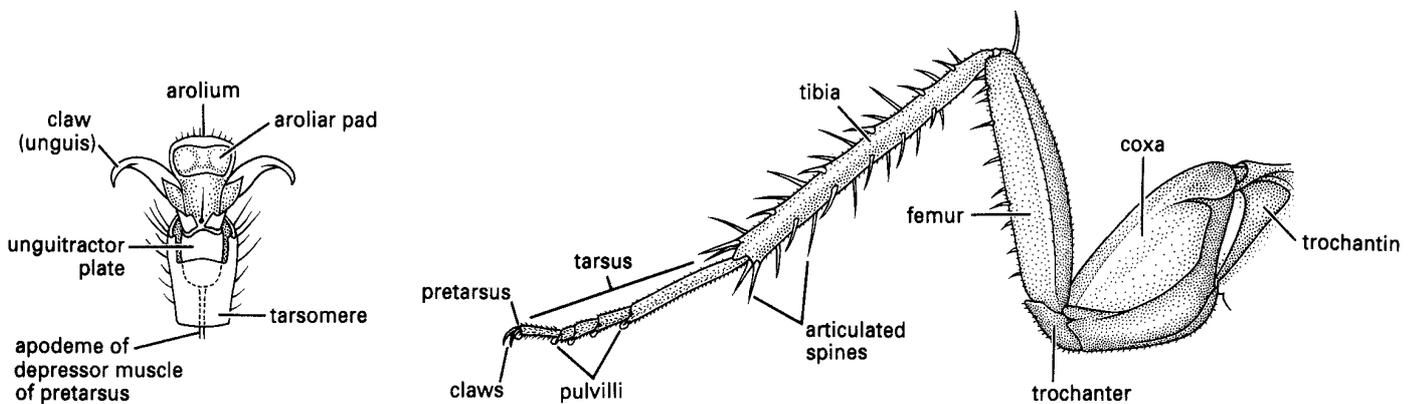


Fig. 2-19: Parts of the generalised walking leg with enlarged ventral surface of pretarsus and last tarsomere shown on the left (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

2.1.3.2 Wings

The wings of insects are unique structures not found in other organisms. The wing of a bird or a bat is a modified foreleg, whereas the insect wing is an outgrowth of the body wall. Wings have no muscles attached inside them. Wings, giving the power of flight, are one of the most important reasons for the evolutionary success of insects.

The winged insect (**Pterygota** = wing) usually has two pairs of wings attached to the **meso-** and **metathorax**. Wings are thin, flap-like extensions of the body wall with an upper and lower membrane and a set of strengthening veins and cross-veins, as shown in **fig. 2-21**, which are important diagnostic features.

Wings usually can be folded, except in **Palaeoptera** (= old winged) orders like damselfly and dragonflies (**Odonata**). Usually wings are transparent but in butterflies and moths (**Lepidoptera** = scale wings) they are covered with scales. The first pair of wings in beetles (**Coleoptera** = cover wings) is reduced to hardened wing covers (**elytra**), to protect the second pair of wings during rest. The leathery, hardened forewings of earwigs (**Dermaptera** = skin-like wings) and grasshoppers (**Orthoptera** = straight wings) are called **tegmen**. In flies (**Diptera** = two wings only) the second pair of wings is reduced to a pair of slender knobbed balancing organs called **halteres**. Insect orders of the **Apterygota** (= no wings) are primarily wingless, whereas in some **pterygote** orders the wings are reduced secondarily, like in fleas

(**Siphonaptera**) and lice (**Phthiraptera**). The fore- and hindwings of most moths are hooked together by a **frenulum** or wing-coupling mechanism, as shown in **fig. 5-49**. Thus the flight of moths is stabilised and the flight performance enhanced compared to butterflies.

2.1.4 Abdomen

The abdomen is the posterior body region of an insect. The generalised insect abdomen is composed of eleven or fewer rather uniform segments with the last segment forming the appendages. Many insects have eight or fewer segments due to fusion. The abdominal segments are composed of **tergites** (**terga** or dorsal plates) **sternites** (**sterna** or ventral plates), and a connecting **lateral membrane**, as shown in **fig. 2-22**. One pair of **spiracles** can be found laterally on the first eight segments. The spiracles are openings of the **tracheal system**, the 'respiratory' system of insects. The anus is housed in segment 10. Adult insects lack abdominal legs but these **false legs** can be found for instance in some caterpillars. Many insects however have a number of appendages at the posterior end of the abdomen homologous to the true legs of the thorax. Appendages of a non-reproductive nature like the tactile organs on the terminal segment are called **cerci**. Reproductive appendages, form the **ovipositor** in females for laying eggs and **copulatory organs** in males.

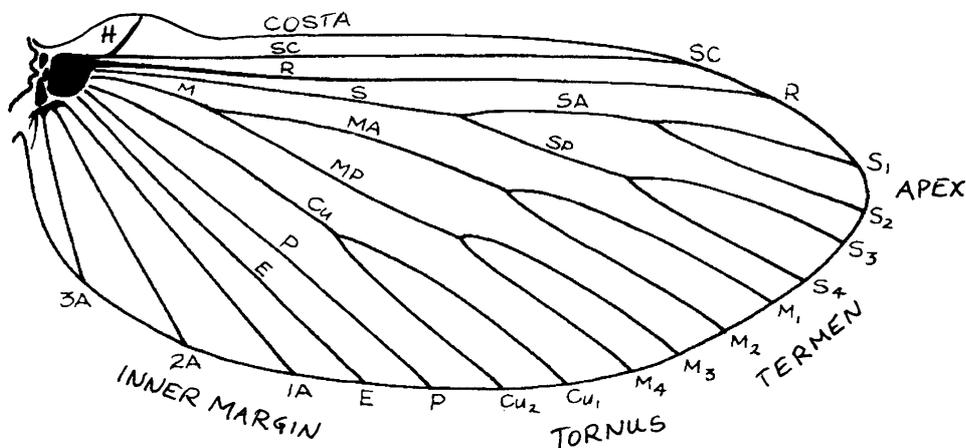


Fig. 2-21: Venation of an insect wing **H:** humeral vein, **Sc:** subcosta, **R:** radius, **S:** sector, **M:** media, **Cu:** cubitus, **P:** plical vein, **E:** empusal vein, **1A, 2A, etc.:** anal veins (reproduced from Ross, H.H. et al., 1982)

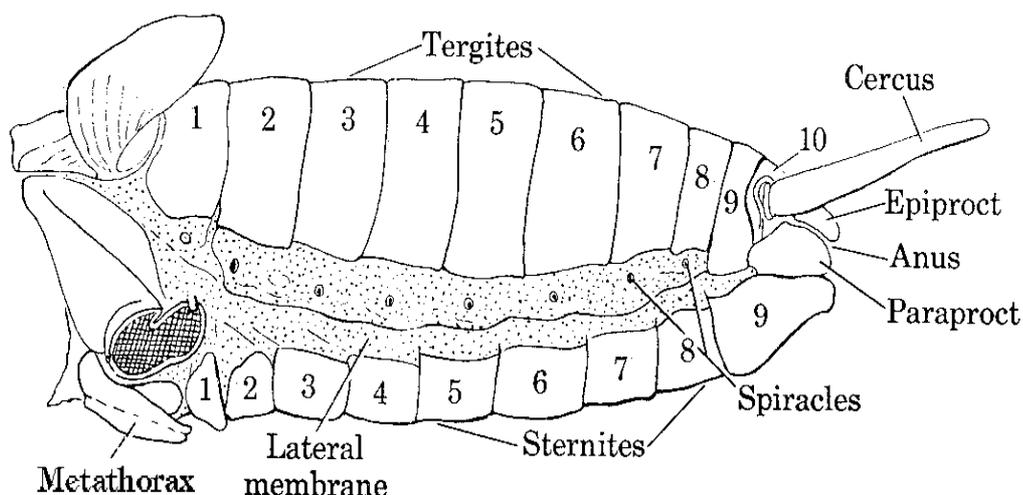


Fig. 2-22: Abdomen of an insect (reproduced from Ross, H.H., et al, 1982)

2.2 Internal Anatomy and Life Processes

Compared to vertebrates, insects are tiny little creatures. Despite their small size, they are very complex organisms, composed of millions of cells. Insects like vertebrates possess a heart, a brain, intestines, muscles, sense organs and other highly specialised organs and tissues. Their senses are in many regards much more outstanding, subtle and sensitive than the senses of most other animals. Insects develop from an egg cell via several larval instars, appearing to be completely different life forms from the adults at the end of the development. One advantage of being small in size is the insects' rapid development, which takes in some cases only a few days for the egg to turn into an adult. The price for it however, is a generally short lifespan.

2.2.1 Digestion and Excretion

Living organisms continuously require energy to maintain vital functions. The energy is generated by a process called **respiration** in which nutrients are oxidised in cells using molecular oxygen. The nutrients are supplied by food, but most of the substrates have to be broken up during digestion. The insect's

digestive or intestinal tract is divided into three specialised major parts, the **foregut**, **midgut** and **hindgut** as shown in **fig. 2-23**.

The food is gathered and prepared by the mouthparts. Prior to ingestion, the food undergoes the enzymatic effects of **saliva** either in the mouth or externally. The **pharynx** and **esophagus** carry the food to the muscular **crop** located in the **foregut**. There the food is subject to further mechanical break-down in this so-called 'gastric mill'. The **midgut** is the organ corresponding to a vertebrate's stomach. Acid and enzymes of the digestive juices are produced and released by the **gastric caeca** to degrade proteins, fats and carbohydrates into their respective smaller compounds, ie. amino acids, fatty acids and sugars. The **Mid-** and **hindgut** are responsible for the up-take of the nutrients. A further task of the latter part is to absorb water and thicken the contents of the guts for final excretion of faeces.

The **Malpighian tubules** drain between the mid- and hindgut. Their primary function is, in analogy to the vertebrate's kidneys, the elimination of 'waste' from the insect blood (**hemolymph**). These 'wastes' are particular metabolic end products such as ureic acid, excess water and minerals. The **fat body** coats the guts and is closely associated with muscles. It fulfils the functions of the vertebrate's liver as the central metabolic organ and energy store.

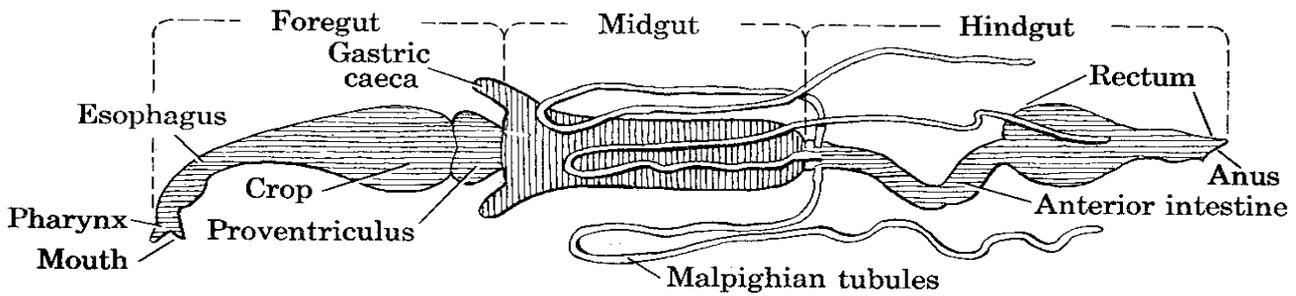


Fig. 2-23: Subdivisions and outgrowths of an insect's alimentary channel (reprod. f. Ross, H.H. et al., 1982)

2.2.2 Circulatory System

Vertebrates have a closed circulatory system of blood vessels with **arteries**; **veins** and **capillaries**. In insects however, 'blood' or **hemolymph** is simply flowing through the body cavities driven by a primitive tube-like heart located in the dorsal part of the abdomen as shown in **fig. 2-24**. This **dorsal vessel** is the only blood vessel in the insect body. Haemolymph from the abdominal body cavity, rich in nutrients, enters the dorsal vessel through valve-like openings, the **ostia** and is then pumped towards the head. Apart from the heart, independent **accessory pulsatile organs** can be found at the base of the antennae and legs to enhance their supply of blood.

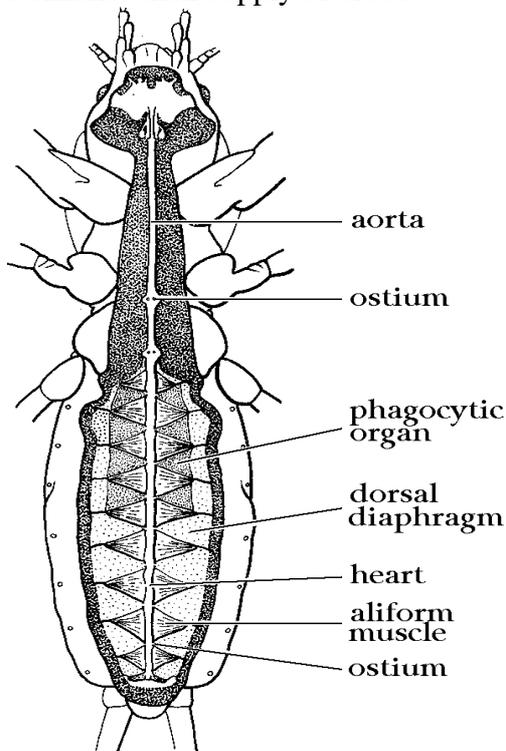


Fig. 2-24: The dorsal blood vessel or 'heart' of an insect (reproduced from CSIRO, 1991)

The major function of the hemolymph is the supply of various organs and tissues with **nutrients**. Furthermore blood is the carrier of **hormones** and other transmitters and has to remove **metabolic end products**. Another function is to maintain a certain internal hydraulic pressure, supporting the exoskeleton in its task of keeping the body in shape.

The hemolymph consists of a liquid part, the **plasma** and of cellular compounds called **hemocytes**. The latter are responsible for the insect's **immunity** and **wound healing**. The hemolymph usually has a greenish-yellow, transparent colour and does not contain any respiratory pigments. In vertebrates oxygen is transported by the pigment **hemoglobin** located in red blood cells, but in insects the oxygen is supplied directly to tissues via the **tracheal system** and not via the blood.

2.2.3 Gas Exchange

Heterotrophic organisms like insects require molecular oxygen for a process called **respiration**. During this process nutrients are oxidised for energy generation and water and carbon dioxide are produced. Therefore oxygen has to be supplied and carbon dioxide removed continuously.

For the purpose of **gas exchange** insects possess a system of hollow tubes called **tracheae** (**fig. 2-25**). Distally the tracheae open into the paired **spiracles** found laterally on most thoracic and abdominal segments as shown in **figs. 2-22, 2-25** and **2-26**. The proximal ends of the tracheae form narrow branches or **tracheoles** that are closely associated with the internal organs and tissues.

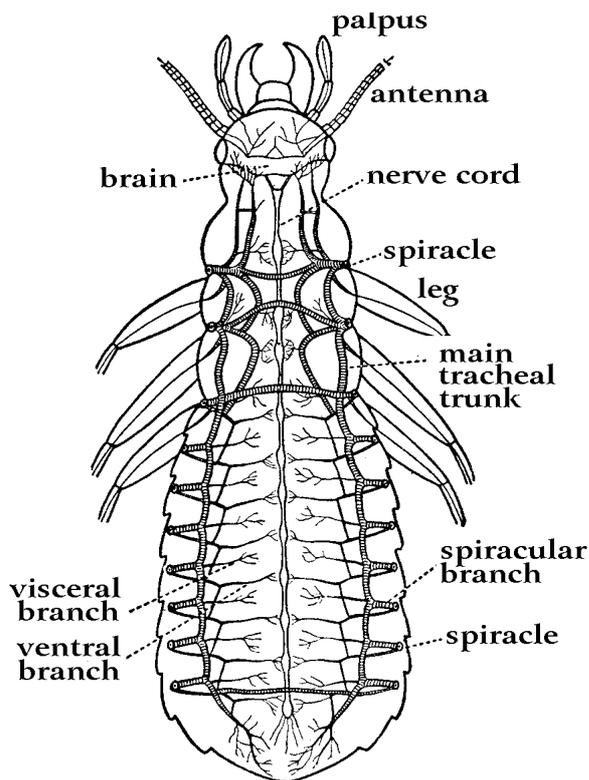


Fig. 2-25: The tracheal system of an insect (reproduced from Ross, H.H. et al., 1982)

Oxygen passively moves from outside through the tracheae to all parts of the body, where it is required for the essential respiratory process. Carbon dioxide in return, also moves passively from the inside to the outside.

The driving force for gas exchange is **diffusion** and to a certain extent squeezing of gases by movement of the body. Insects are restricted from growing larger than 20 cm, since there is no active ventilation system like in amphibians, reptiles, birds and mammals.

Aquatic insect larvae possess **gills** for gas exchange with the surrounding water. Others like adult water beetles carry an air bubble entrapped between the elytra and the abdomen.



Fig. 2-26: Abdominal spiracles of *Theretra* sp. (Sphingidae) (photo Schneider, M.F.)

Most animals are highly susceptible to oxygen deficiency (**anoxia**) and usually die after a few minutes without an oxygen supply. Insects however can sustain anoxic conditions for a very long time without being harmed. Carbon dioxide on the contrary can be used as a sedative, reversibly putting an insect to sleep for a while.

2.2.4 Nervous System

Insects have a highly developed nervous system whose outstanding abilities to coordinate senses, muscles, etc. are demonstrated impressively for instance by the flight performance of dragon flies and damsel flies (**Odonata**).

The basic unit of the nervous system is the **nerve cell**. Millions of such nerve cells are linked together for information exchange like in a tremendously complex computer network. A nerve cell has long extensions (**dendrites**) that transmit the information as electrical current to other nerve cells or muscle cells, like a power cable. The **neurotransmitter acetylcholine** then carries the signal through a tiny **synaptic gap** between the membranes of the sending and receiving cell. Certain chemical insecticides like **organophosphates** specifically interfere with the process of signal transduction between nerve cells and as a result paralyse and kill target insects.

The nervous system consists of a **central nervous system** and **stomodeal nervous system**. The central nervous system is composed of the **brain** as major coordinating organ located in the head plus paired nerve centres per segment called **ganglia**. Brain and ganglia consist of masses of nervous tissue joined together by **nerve cords**. The ganglia are fused in some insects as shown in **fig. 2-27**.

The **stomodeal** or **stomatogastric nervous system**, also referred to as the **sympathetic nervous system**, controls involuntary motions of parts of the guts and the dorsal blood vessel. This part of the nervous system is located in front of the brain and next to the esophagus.

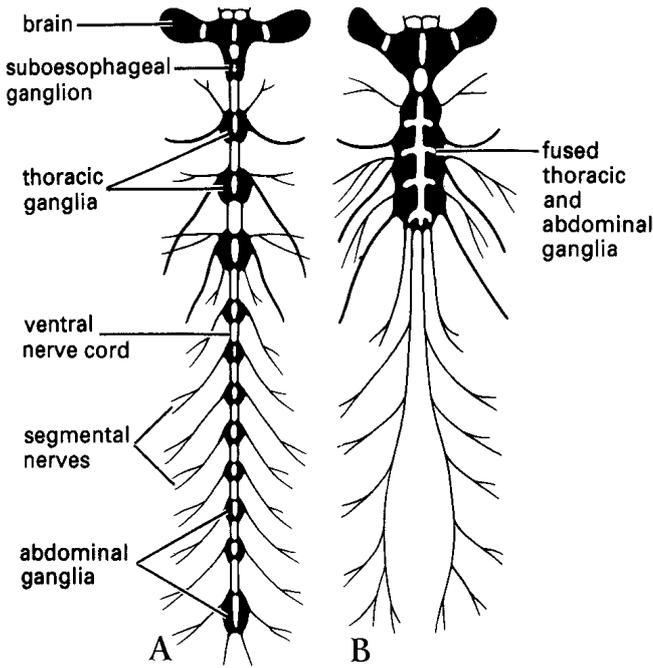


Fig. 2-27: The central nervous system of insects with brain and several ganglia (A) and fused ganglia (B) (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

discovered so far. Some important hormones are **Ecdysone** produced in the paired **prothoracic glands** and **Juvenile Hormone** produced in the paired **corpora allata**. Both hormones play an important role in controlling the moulting process during the development of insects as further outlined in **chapter 2.2.9**. Others are smaller neuropeptides like **Adipokinetic Hormone** which controls lipid and carbohydrate metabolism eg. during sustained flight and **Diapause Hormone** which activates dormancy in insect eggs.

Exocrine Glands

Unlike endocrine glands, **exocrine glands** release their products to the outside of an insect. Main glands of this type are for instance the **salivary glands** which are located in the thorax and drain saliva with digestive enzymes into the mouth. **Scent glands** like **pheromone glands** or **stink glands** and other defensive glands have openings dispersed over the cuticle. Scent glands are further discussed in **chapter 3.1.3**.

2.2.5 Endo- and Exocrine System

Endocrine or Hormon System

Physiological as well as behavioural responses of insects are controlled by the central nervous system in conjunction with the **endocrine** or **hormonal** system. Central nervous stimuli usually cause instant reactions such as the reflex of an insect escaping upon disturbance. Endocrine control is often effective within the range of minutes or hours thus controlling medium or long term processes.

Endocrine glands or **hormone glands** shown in **fig. 2-28** produce messengers called **hormones** or **neuropeptides**, that are released into the haemocoel and carried by haemolymph to the respective target organs. There have been almost thirty insect hormones

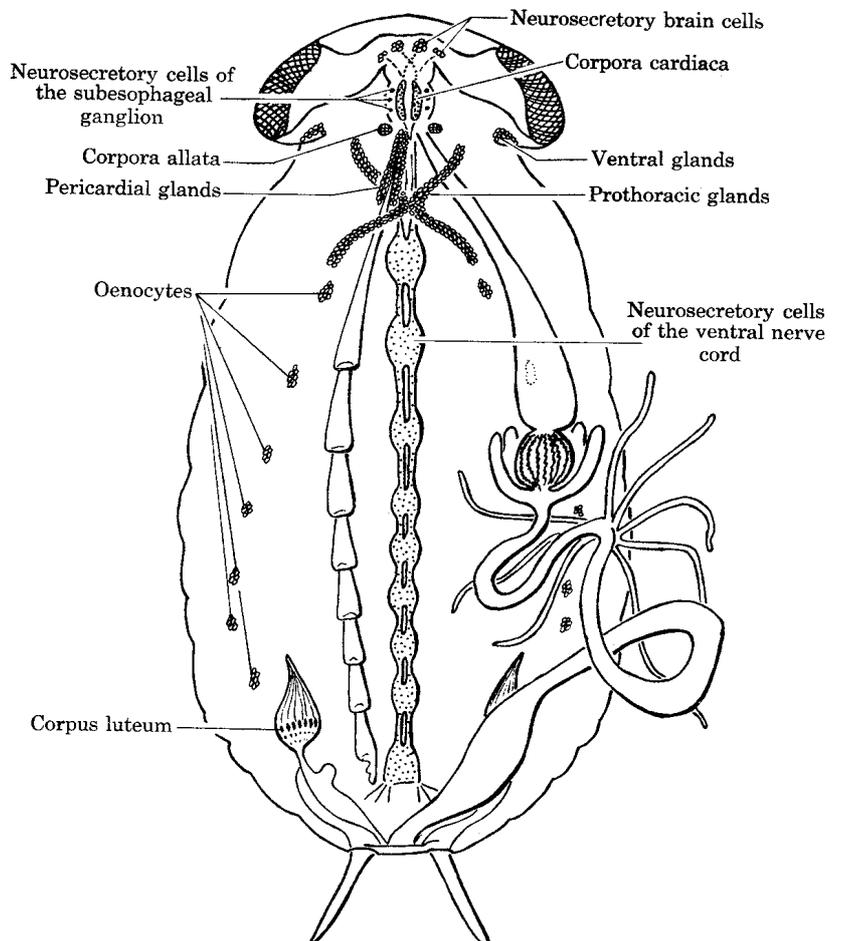


Fig. 2-28: Secretion sites of the main insect hormones (reproduced from Ross, H.H. et al., 1982)

2.2.6 Sense Organs

Insects can perceive light, sound, scent, gravity and temperature in minute quantities often far beyond what can be detected by other animals. The subtle chemical sense of some moths for instance, allows the males to sense a female from as far away as one kilometre. Ticks and fleas can sense even the slightest changes of temperature in the environment caused by the body temperature of a mammal passing by at some distance and eventually jump onto the host. An attempt to kill a fly with bare hands is almost impossible since it reacts much faster than our hands can strike.

Mechanoreception

Mechanoreceptors are stimulated by sound waves, vibrations and touch. **Touch** is monitored by hair-like **trichoid** sensilla or **setae**, shown in **fig. 2-3**, scattered over the surface of the body and appendages like antennae, cerci and tarsi. **Hearing** is the ability to perceive sound waves that either stimulate trichoid sensilla as shown in **fig. 2-3** or membrane-like structures. The latter type is called the **tympanal organ** and can be found on the tibiae of **Tettigoniidae** forelegs (**fig. 2-29**), on wings of some moths, on the thorax of noctuid moths and on the abdomen of some other insects. The membrane or **tympanum** swings as a result of the impact of sound waves like the membranous skin of a kundu drum when held close to a speaker. The movement of the membrane is then transformed into a nervous signal. Often the tympanal organs are closely associated with other structures like the tracheal system as shown in **fig. 2-29** in order to enhance sound reception. Some insects like noctuid moths are able to detect ultra sound produced by bats (see **chapter 4.4**).

Vision

Most adult insects and larvae have a pair of **compound eyes** and up to three **ocelli** or simple eyes, as shown in **fig. 2-30**. The compound eyes are complex and variable. Generally they are large and located at the top and to the sides of the head. Each compound

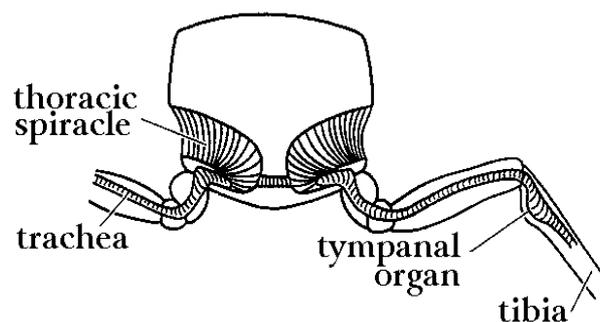


Fig. 2-29: Tympanal organ on the tibia of a grasshopper's foreleg associated with tracheal system (reproduced from CSIRO, 1991)

eye is composed of individual sensory units called **ommatidia**. The number of ommatidia varies from one in some ants to 30,000 or more in some flies, beetles, and dragon flies. Each ommatidium contains a lens and sense cells

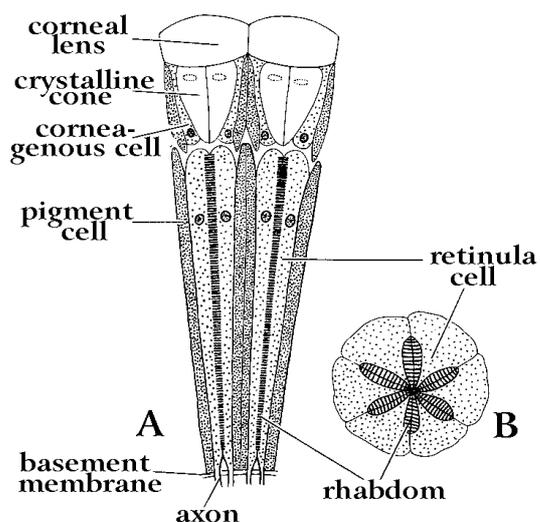
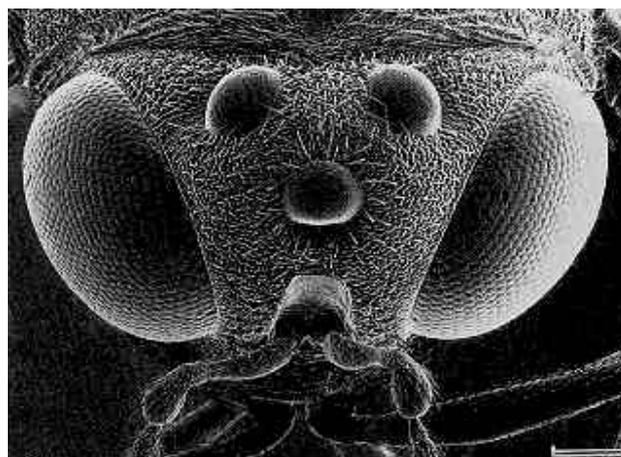


Fig. 2-30: Compound eyes and ocelli of a hymenopteran insect (top) and longitudinal section (A) and cross-section (B) of an ommatidium (bottom) (reprod. from CSIRO, 1991)

(**pigment cells**). The process of photoperception happens in the pigment cell, that converts light into nerve signals. An individual ommatidium can perceive only a small portion of the environment. However the combined images of all ommatidia form a mosaic view of the insect's environment. Most adult insects and larvae have simple eyes, called **ocelli**, located on the dorsal portion of the head. The number of ocelli can vary from zero to three, depending on the taxon. Their function is not fully understood. They are not important as image formers but are light sensitive and act as 'stimulatory organs' in reaction to major changes in illumination.

The colour spectrum seen by insects often exceeds the range of light visible for humans. Bees for instance are able to detect ultraviolet light (UV), invisible for humans. Apart from that, bees are also able to sense polarised light, as further outlined in **chapter 3.2.2**.

Chemoreception

Chemoreceptors respond to chemical aspects of the environment, **taste** and **olfaction** are chemosenses. Chemoreceptors for taste are abundant on mouthparts and other body parts like tarsi. The receptors for smell are located on the surface of the cuticle and antennae. These **olfactory** sensilla are highly sensitive to specific scents. Male moths can perceive **pheromones** released by females in minute concentrations, amounts so small that they cannot be detected by the most sophisticated analytical devices of chemists. The outstanding olfactory abilities of insects are further outlined in **chapter 3.1.3**.

Thermoreception

The sense for temperature is housed in antennae and other appendages of the head. Qualities like warm and cold are most important for **poikilothermic** organisms like insects that cannot maintain a constant body temperature. Therefore, insects try to find an ambient environment, for instance in the shade, if it is hot, in order to keep the body at a suitable temperature. During early morning hours butterflies can be observed, spreading and directing their wings towards the sun so

that the radiant solar energy influences their body temperature. Another possibility of **thermoregulation** is to generate warmth by means of the flight muscles. Due to the high metabolic rate of some moths so much heat is produced that it can raise their body temperature up to 10 °C higher than the surrounding environment.

The temperature optimum of insects lies between 21 °C and 35 °C. Usually insects can't survive temperatures above 42 °C. Tropical species can be also very susceptible to low temperatures, and might die, when the temperature drops below 10 °C. Insects of temperate areas are inactive and hibernate during the coldest months of the year. They can survive temperatures of a deep freezer and die if it becomes colder than -30 °C.

2.2.7 Locomotion

There is hardly any locomotive action that cannot be performed by insects: they can fly, swim, dive, jump, walk, run, creep and dig. Movement requires the action of muscles of which an insect houses a considerable number in its body and limbs. For instance inside a grasshopper's jumping leg, as shown in **fig. 2-31**, a complex system of muscles can be found.

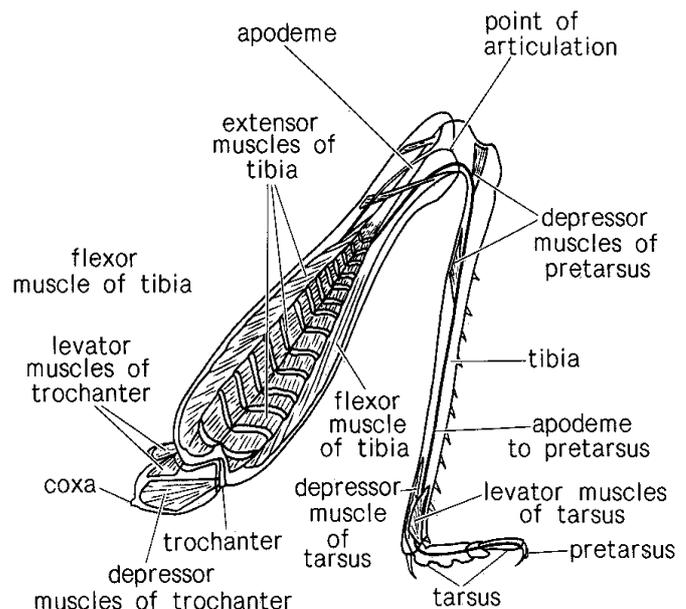


Fig. 2-31: Jumping hindleg of a grasshopper showing arrangement of muscles (reproduced from CSIRO, 1991)

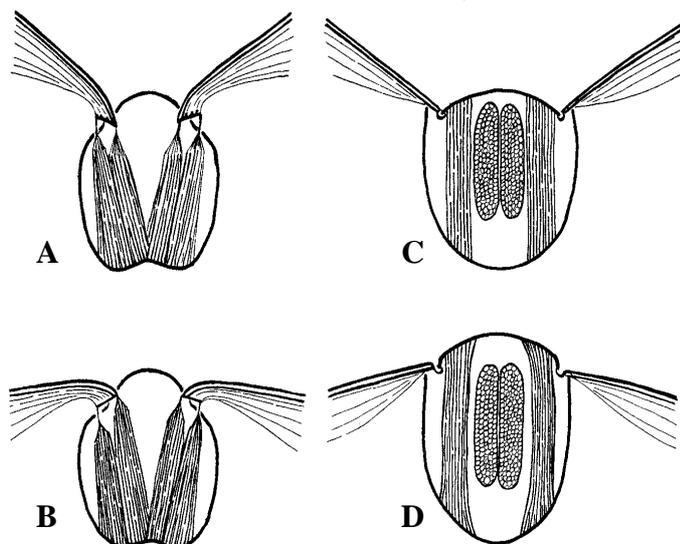


Fig. 2-32: Direct (A, B) and indirect (C, D) flight muscles of insects (reproduced from Ross, H.H. et al., 1982)

The massive flight muscles occupy most of the space in the wing-bearing segments of the thorax. There are two different systems, the **direct** and **indirect** flight muscles as shown in **fig. 2-32**. The direct flight muscles as found for example in dragonflies, are directly attached to the wings. A contraction of the inner dorso-ventral muscles moves the muscles upward, whereas a contraction of the outer pair of muscles forces the wings downward. In the case of indirect flight muscles, which are not directly attached to the wings, a contraction of the dorso-ventral muscles results in a depression of the tergum, lifting the wings up, whereas a contraction of the longitudinal muscles 'pops' the tergum out resulting in a downward movement of the wings. This type can be found for instance in houseflies.

A further distinction can be made between **synchronous** and **asynchronous** flight muscles. Synchronous muscles require one nervous impulse per contraction whereas asynchronous muscles contract several times per nervous impulse. A nerve cell needs to recover for about 100 msec or $\frac{1}{10}$ of a second (**refractory period**) before it can 'fire' again. This fact makes asynchronous muscles much faster. Therefore, insects with a rapid wing beat frequency like houseflies possess asynchronous flight muscles.

2.2.8 Reproduction

Insects have developed quite a number of sexual and asexual mechanisms for the production of offspring.

The major case is **sexual reproduction**, the fusion of a **haploid egg** cell with a **haploid sperm** cell, resulting in a **diploid fertilised egg** cell. The advantage of sexual reproduction is **reshuffling** of genes with the outcome of producing genetically diverse and different offspring.

The paired glands producing the reproductive products - either sperm or eggs - are called **gonads** and are shown in **fig. 2-33**. Sperm or semen is produced in the male **testes**, whereas egg cells, also called **oocytes**, are produced in the female **ovaries**.

Copulation is often introduced with **courtship** behaviour like the 'dancing' of butterflies or particular calls of crickets. During **copulation** or **insemination** the male animal transfers **sperm** into the **vagina** of a female. Various specialised reproductive appendages of the male and female abdomen are involved in the process of copulation. The sperm might be temporarily stored in the **spermatheca** or **receptaculum seminis** of the female, shown in **fig. 2-33**. Termite queens can store sperm and keep it alive for a considerable time, up to many years and are consequently independent of further contact with males.

During **ovulation**, the mature egg cells leave the ovaries and pass through the **oviducts**. Then the egg cells are **fertilised** by a small amount of sperm released from the spermatheca. Thus, copulation and fertilisation are independent of each other and do not necessarily have to take place at the same time.

After the fertilisation of the eggs, females of most insects lay the eggs (**oviposition**). The successive process of ovulation, fertilisation and oviposition is called **oviparity**. Oviposition is carried out in various ways. Females of some species possess **ovipositors**, enabling eggs to be laid into soil or injected into fruits or other hosts. Eggs are either laid singly or in clusters. The latter might be

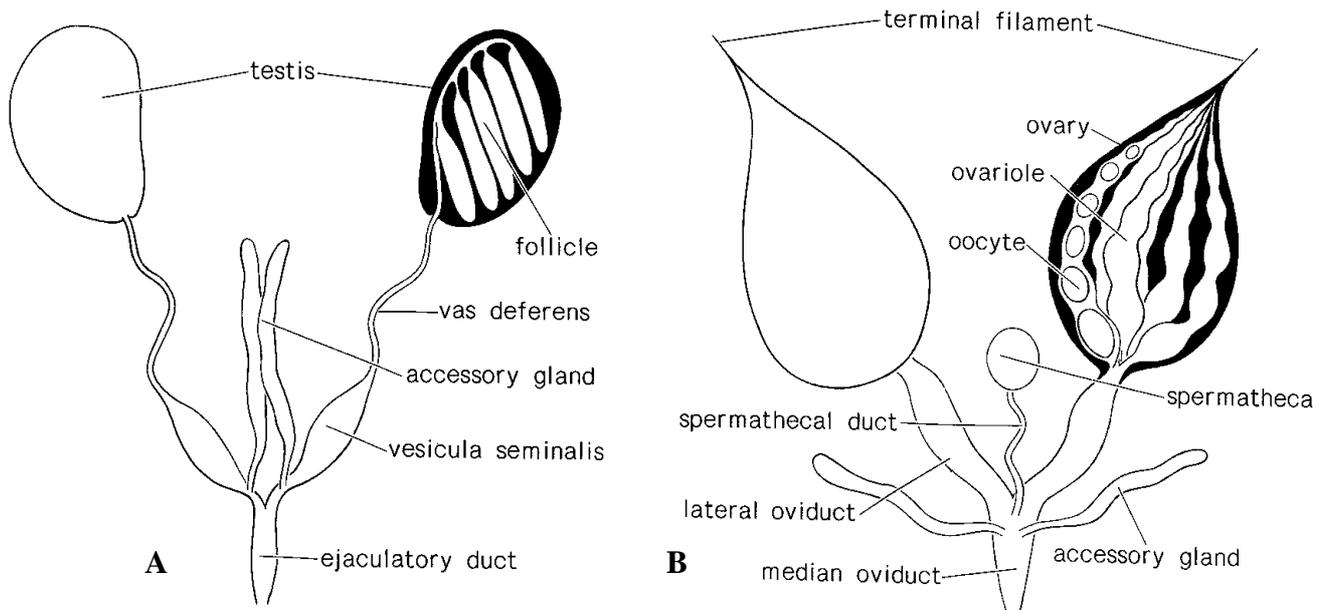


Fig. 2-33: Male (A) and female (B) reproductive system (reproduced from CSIRO, 1991)

enclosed in spittle masses produced by spittle bugs or in foam-like pods made from protein, called **ootheca** as is done by praying mantids, locusts and cockroaches. Eggs can be glued onto a substrate such as leaves and bark, but are always laid on or at least in close proximity of the larval source of food. Female butterflies and moths lay their eggs on the respective food plants of the caterpillars. A female Birdwing for instance carefully checks a potential *Pararistolochia* or *Aristolochia* plant, before she lays the eggs. She makes sure, that there are enough young and soft leaves available for the developing caterpillar. The female also looks for the presence of other eggs in order to avoid competition between the caterpillars. Finally she lays one to two eggs on the underside of a leaf, so that the eggs are protected from sun and rain and hidden from egg parasites.

Such care-taking actions of females ending right after oviposition are called **brood care**. **Parental care** refers to the actions of parents after the laying of the eggs, for protection of the brood and provision of food. Parental care is common for example in social insects, spiders and cockroaches and as shown in **fig. 2-34** in Harlequin bugs.

Apart from oviparity, there are several less common but very interesting strategies of

viviparity. Eggs of **ovoviviparous** species are incubated in the reproductive tract of the mother for a certain period of time. In the case of viviparity the incubation time is extended and eventually ‘birth’ is given to larvae. Some strange and rare cases of **adenotrophic viviparity** occur in some flies. The poorly developed larvae hatch in the ‘uterus’ and orally feed from ‘milk’ glands of the female’s reproductive system. The fully developed larvae are then deposited and pupate instantly. Embryos of **haemocoelous viviparous** Strepsiptera develop in the haemolymph of the female. The larvae leave the mother through a brood canal. A really alienating case of haemocoelous viviparity are the larvae of particular gall midges (Diptera) that develop in the mother and subsequently consume her.

The second basic reproductive strategy apart from sexual reproduction is **parthenogenesis**. It is a form of asexual reproduction that can be found for instance in some cockroach, wasp, bee and ant species. These females can produce offspring without being fertilised by males. The involved egg cells are then not subject to **meiosis** as they remain **diploid** and therefore do not require any fertilisation. The price for being independent of males is, that only genetically identical individuals (**clones**) or at

least individuals without great genetic variation are produced. Parthenogenesis might be obligatory or facultative and result in the production of female or male eggs only. Females of **partial parthenogenetic** species produce mainly parthenogenetic generations of females only. Occasionally generations of both males and females are produced sexually. Other asexual strategies are **hermaphroditism**, **polyembryony** and **paedogenesis**.

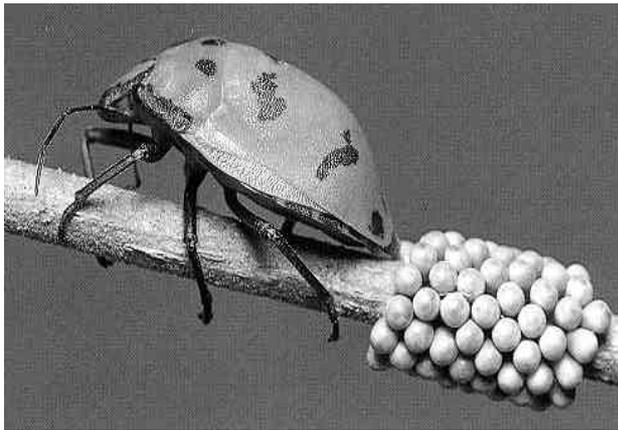


Fig. 2-34: Female *Tectocoris diophthalmus* (Hemiptera: Scutelleridae) guarding her eggs (reproduced with permission from Monteith, G., 1991)

The **sex** of most insects is genetically determined by the number of **sex** or **X- chromosomes (heterochromosomes)**. Usually females possess two X-chromosomes (**XX**) whereas males have one only (**X0**), but this allocation varies between taxonomic groups. A less common sex determination system found in bees amongst others, is called **haplodiploidy**. Female bees develop from fertilised eggs and are thus diploid. The male **drones** are haploid, have only one set of chromosomes and develop from unfertilised eggs. Haplodiploidy allows the bee's queen to control the sex of her offspring by fertilising eggs to produce females. In humans, by the way, two heterochromosomes, **X** and **Y** can be found. The combination of **XX** results in females, whereas **XY** results in male humans.

The large number of eggs as well as the short generation time is the major reason for the reproductive potential of insects.

2.2.9 Development

Ontogeny is the development of an **egg** through several stages into an **adult** or **imago**. During development tissues differentiate and an insect gains size. The fully sclerotized cuticle of an insect is inflexible and rigid, so that it cannot grow any more (see **chapter 2.1.1**). Therefore the insect has to undergo several **moult**s during its development, i.e. to produce a new expandable cuticle and to cast off the hardened cuticle of the previous stage. Prior to each moult, a new cuticle is growing below the old one. Then the latter separates from the newly formed cuticle, during a process called **apolysis**. Finally during **ecdysis** the old cuticle dorsally opens up to release the next stage and the old cuticle (**exuviae**) is cast off. Initially the cuticle of the newly emerged insect is soft and flexible. Thus the ecdysed insect is able to pump air into its trachea in order to gain body size, like inflating a balloon. According to **Dyar's law**, the increase in size from instar to instar is often of the factor 1.4. After each moult the cuticle hardens or **sclerotizes**, a tanning process which takes from thirty minutes up to several hours. During this time the insect has to hide since it is quite vulnerable, e.g. to predation and desiccation. The development of an insect takes from about one week to several years and depends on the size of the insect and the surrounding temperature. Generally the larger the insect is the longer it takes for its development.

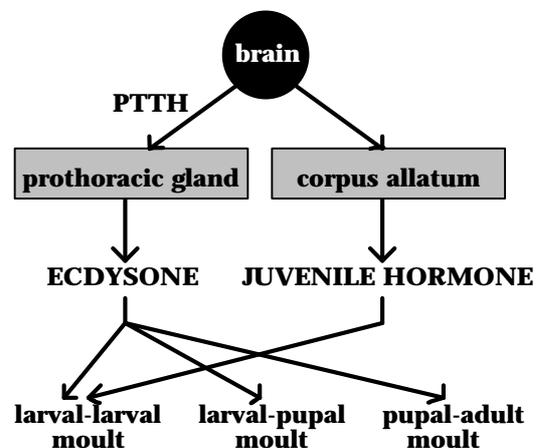


Fig. 2-35: Simplified diagram of the endocrine control of moulting and metamorphosis in endopterygote insects; for more information see text

Moulting is a complex process that is controlled by three major hormones as shown in **fig. 2-35**. **Ecdysone** is produced in the prothoracic glands and released upon stimulus by **Prothoracicotrophic Hormone (PTTH)**. Each moult is mediated by **Eclosion Hormone** and Ecdysone. The presence of **Juvenile Hormone** suppresses the final moult in larval instars, its absence makes a larval instar turn into a pupa or an adult.

Three different major patterns for the development from the larva to the adult insect can be found. The primitive **ametaboly** is without marked change in form. Insects with **metamorphosis** show a major change in form between immature and mature, winged stages. Metamorphosis can be further divided into partial metamorphosis (**hemimetaboly**) and complete metamorphosis (**holometaboly**). **Box 2-1** summarises differences between hemi- and holometabolous **life cycles** or **life histories**.

Ametaboly without metamorphosis can be found in wingless orders, the **Apterygota** such as silverfish and bristletails. These insects undergo more than ten moults and continue to moult after sexual maturity. There are no marked changes in body form between immature and mature insects.

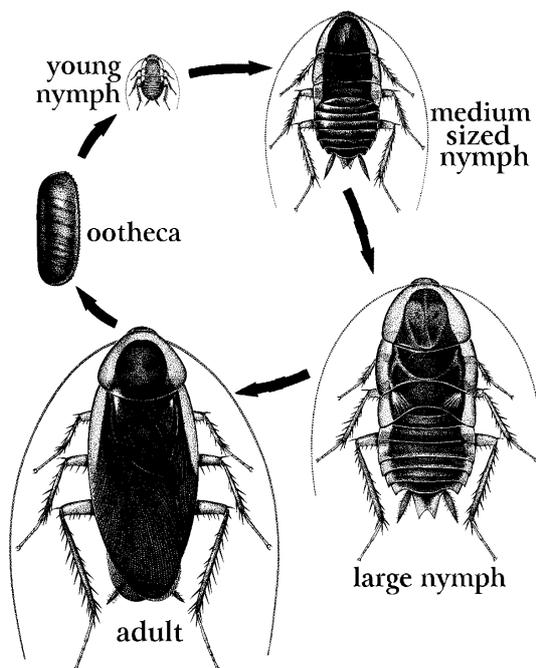


Fig. 2-36: Hemimetabolous life cycle of the cockroach *Methana marginalis* (Blattidae) with gradual metamorphosis (after CSIRO, 1991)

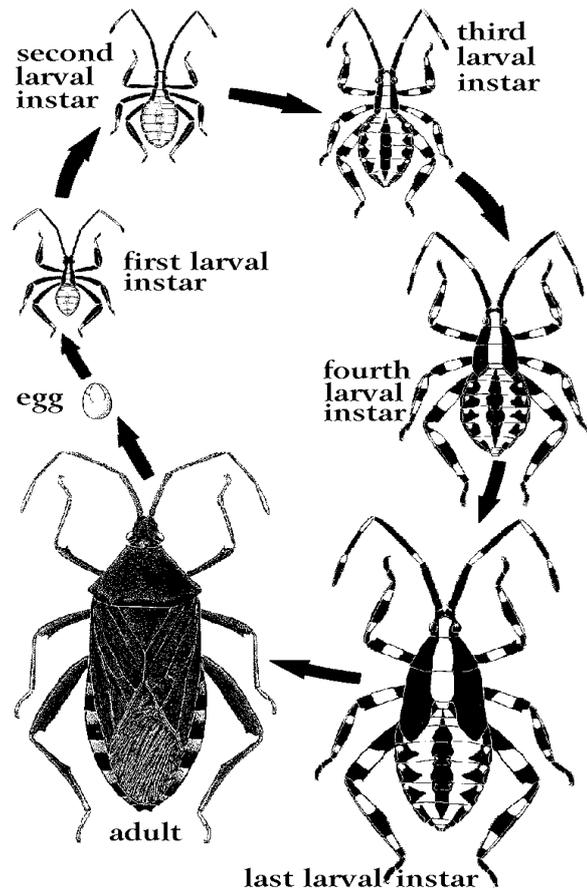


Fig. 2-37: Hemimetabolous life cycle of the hemipteran bug *Amorbus alternatus* (Coreidae) with gradual metamorphosis (after CSIRO, 1991)

Hemimetaboly with partial metamorphosis is a characteristic of dragonflies and damselflies and **exopterygote** insects like locusts, bugs and cicadas. These insects usually have four to five larval instars before they directly change into adults. The larval instars of terrestrial forms are called **nymphs**, those of aquatic insects are known as **naiads**. After each moult wing pads and genitalia increase in size. The immature stages resemble the adults, except that they are smaller and there are no functional wings. Partial metamorphosis can be further divided into **incomplete** (dragonflies, damselflies) and **gradual metamorphosis** (grasshoppers, bugs, cockroaches, etc.). See also **figs. 2-36, 2-37** and **3-9**.

Holometaboly with complete metamorphosis is a feature of **endopterygote** insects whose larvae differ completely from adults as shown in **figs. 2-38 to 2-41** and **6-28 ff**. A caterpillar is very different from an adult butterfly or

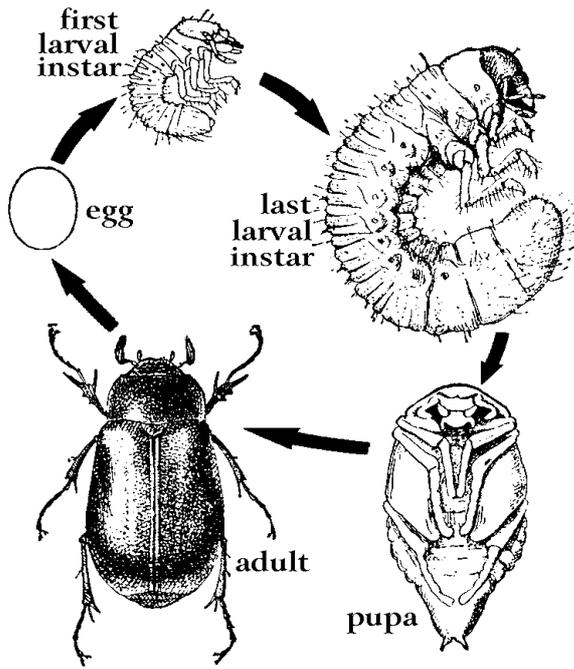


Fig. 2-38: Holometabolous life cycle of the beetle *Phyllophaga sp.* (Scarabaeidae) with complete metamorphosis (after Ross, H.H., 1982)

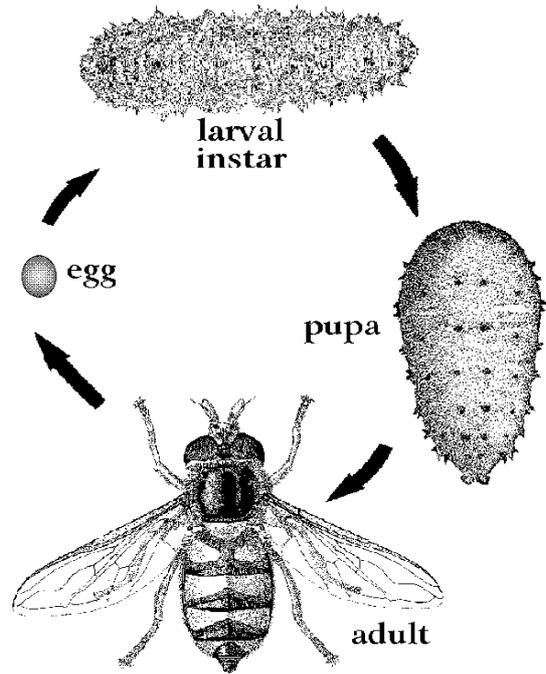


Fig. 2-40: Holometabolous life cycle of the fly *Didea fasciata* (Syrphidae) with complete metamorphosis (reprod. from Ross, H.H. et al., 1982)

moth, a grub does not resemble an adult beetle at all and a maggot differs considerably from an adult fly. There is no progressive change in form towards the adult. Usually four or five, sometimes up to 20 larval instars occur, before the last larval instar turns into the **pupal stage**

or **pupa** from which an adult emerges. The pupa of a butterfly is also called **chrysalis**. The pupal stage is a **resting stage** without feeding and without locomotion but with extensive restructuring of tissues. The pupal stage can last from several days to years.

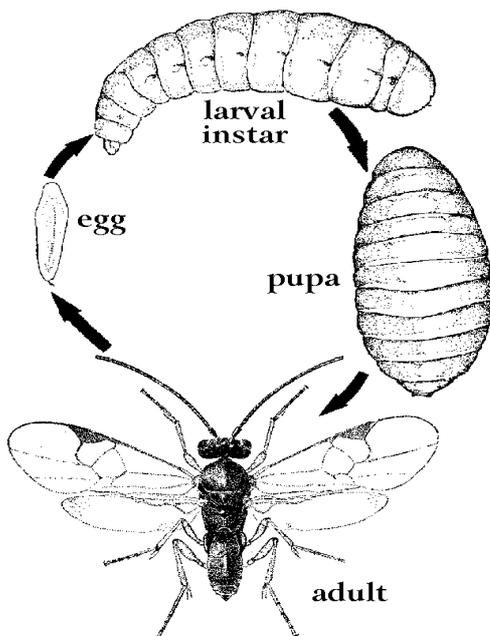


Fig. 2-39: Holometabolous life cycle of the parasitic wasp *Apanteles melanoscelus* (Braconidae) with complete metamorphosis (reproduced from Ross, H.H. et al., 1982)

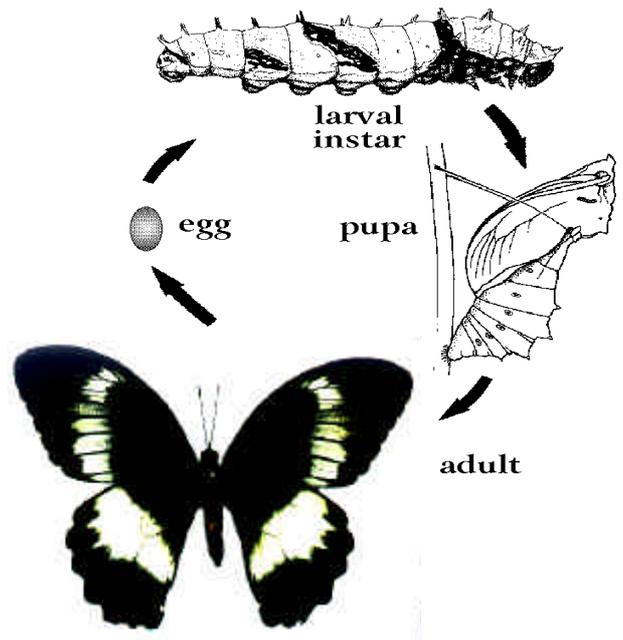


Fig. 2-41: Holometabolous life cycle of the butterfly *Papilio woodfordi* (Papilionidae) with complete metamorphosis (reproduced from CSIRO, 1991; photo Schneider, M.F.)

Hemimetabolous Development	Holometabolous Development
<ul style="list-style-type: none"> • E→L1→L2→L3→L4→L5→A • no pupal stage • wings develop externally (exopterygote insects) • larvae are generally similar in appearance to adults 	<ul style="list-style-type: none"> • E→L1→L2→L3→L4→L5→P→A • pupal stage present • wings develop internally (endopterygote orders) • larvae look very different from adults

Box 2-1: Differences between hemimetabolous and holometabolous development; E = egg; L1 - L5 = larval instar 1 to 5; P = pupa; A = adult

In some holometabolous insect orders a change in the type of mouthparts during metamorphosis can be observed. This is an adaptation to a change of the type of food of the particular instar. Some examples are given in **box 2-2**. Such drastic alterations require a complete metamorphosis and never occur in hemimetabolous insect orders which typically show constancy in this regard.

Since larvae and pupae of holometabolous insects greatly differ from their respective adults, the identification of larvae is often not an easy task. A classification of larvae as suggested in **fig. 2-42** considers more functional rather than taxonomic features.

Polypod larvae possess cylindrical bodies with short thoracic legs and **false abdominal legs**. Most of these larvae are phytophagous and

cannot walk long distances. Commonly polypod larvae can be found in **Lepidoptera**, symphytan **Hymenoptera** and **Mecoptera**. **Oligopod** larvae lack false legs and often have **prognathous** mouthparts. Some are fast predators, others are slowly moving phytophages or detritivores living in soil. Oligopod larvae can be found in most holometabolous orders, but not in **Mecoptera**, **Lepidoptera**, **Strepsiptera**, **Diptera** and **Siphonaptera**. The worm- or maggot-like **apod** larvae lack true legs and live in substrates like soil, mud, dung, rotting plants, carrion or as parasitoids in bodies of other organisms. This type can be found in **Siphonaptera**, aculeate **Hymenoptera**, **Coleoptera** and **Diptera**.

A pupa usually forms in the **puparium**, the hardened cuticle of the final instar larva. The

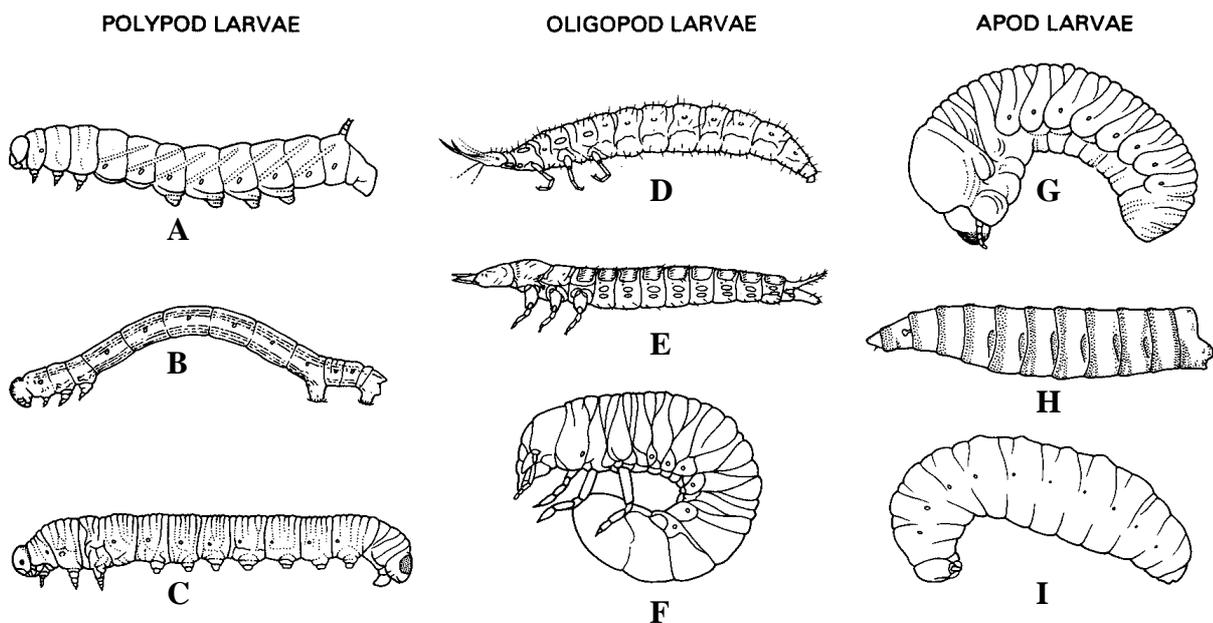


Fig. 2-42: Larval types: polypod larvae (A) Lepidoptera: Sphingidae, (B) Lepidoptera: Geometridae, (C) Hymenoptera: Diprionidae; oligopod larvae: (D) Neuroptera: Osmylidae, (E) Coleoptera: Carabidae, (F) Coleoptera: Scarabaeidae; apod larvae: (G) Coleoptera: Scolytidae, (H) Diptera: Calliphoridae, (I) Hymenoptera: Vespidae (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

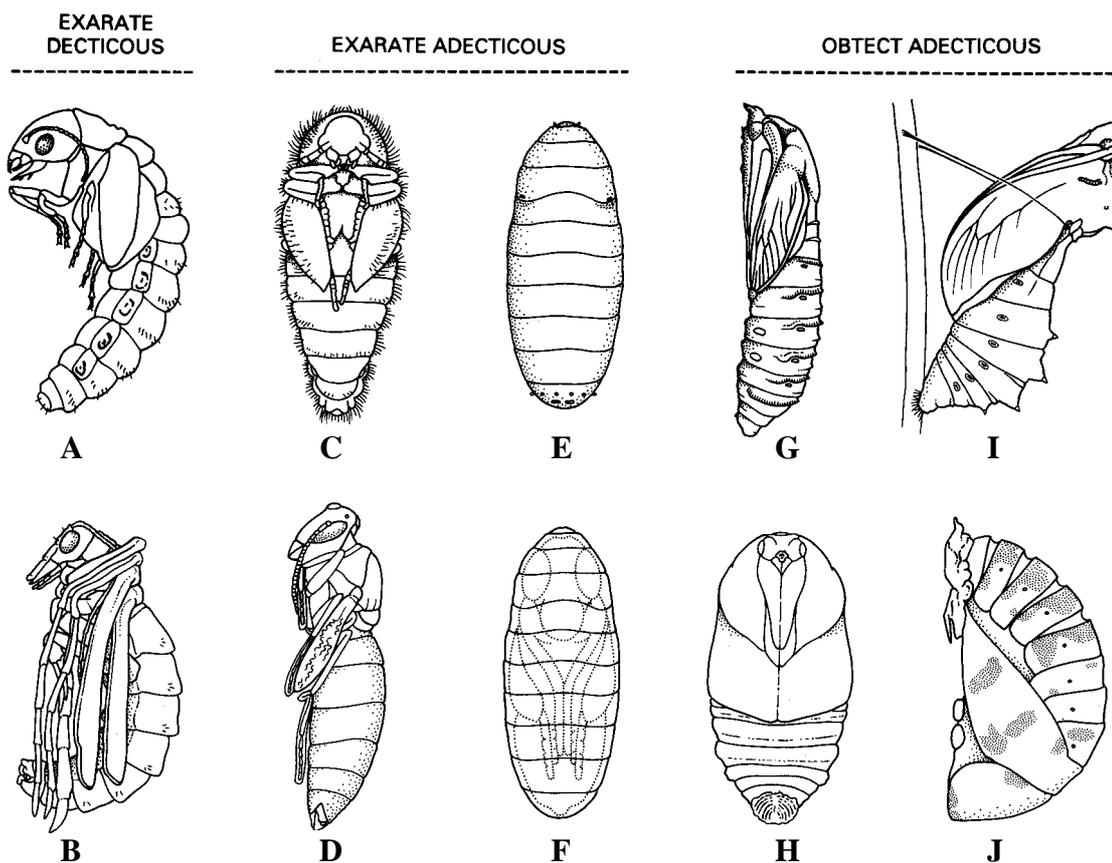


Fig. 2-43: Pupal Types: exarate decticous: (A) Megaloptera: Sialidae, (B) Mecoptera: Bittacidae; exarate adecticous: (C) Coleoptera: Dermestidae, (D) Hymenoptera: Vespidae, (E), (F) Diptera: Calliphoridae; obtect adecticous: (G) Lepidoptera: Cossidae, (H) Lepidoptera: Saturniidae, (I) Lepidoptera: Papilionidae, (J) Coleoptera: Coccinellidae (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

pupa might be surrounded by a cocoon or a protective cell. The fully developed adult that is still enclosed in the puparium is referred to as the **pharate adult**. Most pupae are **exarate**, ie. their appendages like antennae, legs, etc. are free and not fused with the body. **Obtect** pupae have the appendages closely attached to the body. Exarate pupae can be **decticous** with articulated mandibles for biting through and escaping from the cocoon during **eclosion**. Pupae with immovable or non-articulated mandibles are called **adecticous**.

These conditions are important diagnostic tools. Their occurrence within particular insect orders is shown in **fig. 2-43**.

Polymorphism describes the occurrence of morphological variations between individuals of a population and might be of a genetic or environmental nature. Polymorphism can also include physiological, ecological as well as

behavioural differences. Examples for polymorphism like the **cast system** of social insects or the **phase polymorphism** as it occurs for instance in plague locusts are discussed in **chapter 3.2**. Another obvious example is **sexual dimorphism**. It is referred to as distinct sets of phenotypic secondary sexual characteristics for females and males of a species. In other words: a male looks different from a female. Males and females might differ eg. in body size, coloration of body or wings, patterns of songs, presence and shape of wings and appendages like antlers, feelers, etc. Some examples are:

- male stag beetles (**Lucanidae**) have long extended mandibles that the females lack
- only male rhinoceros beetles (**Scarabaeidae**) possess two long horns as shown in **fig. 2-44**
- the antennae of male longicorn beetles (**Cerambycidae**) are much longer than the females' antennae

- the ventral side of the male crusader bug *Mictis profana* (**Coreidae**) is red and has two humps, the underside of the female is brownish and lacks the two humps
- the females of some grasshoppers, stick insects, praying mantids, moths and butterflies like Birdwings are larger than their male counterparts as can be seen in **figs. 2-44** and **plate 7 D** and **E**
- the songs of male crickets and cicadas are different from the songs of their females
- the wing coloration greatly differs between some female and male Lepidoptera like the Birdwings shown on **plate 9**. Other examples are shown on **plates 7 D, E, 8 J, K** and **8 M, N**
- the males of some flies use their antlers or eye-stalks to fight for females, as shown in **figs. 5-45** and **5-46 J, K, L**
- the male stalk-eyed fly *Achias spp.* (**Platystomatidae**) uses its stalked eyes for territorial fights. The eyes of a female are far less modified as shown in **fig. 5-46 J, K**
- the wings of some female cockroach, aphid and praying mantid species are reduced or even absent as shown in **fig. 2-44**
- some male moths (**Lepidoptera**) have enlarged pectinate feelers. This enables them to detect tiny quantities of pheromones released by the females and to eventually meet

them. In the case of *Lymantria ninayi* the larger female has filiform antennae, as shown on **plate 7 D** and **E**.

- the wingless female stylops (**Strepsiptera**) spends all her life as an entomoparasite in insects. The male is much larger and has fully developed wings as shown in **fig. 5-39 B** and **C**
- kings and queens, the male and female reproductives of social insects like termites, ants, bees and wasps look very different. The males are always much smaller. **Fig. 2-44** shows the difference between a termite queen and king

The development of an insect markedly depends on a set of environmental factors like humidity, temperature and photoperiod or day length. Each of these **abiotic factors** on its own or in conjunction with other factors can directly or indirectly influence insect development. Temperature for instance can have an effect either on the availability of foodplants or on the temperature-dependent biochemical processes during the complex life cycle of **poikilothermic** insects. Biotic and abiotic effects are outlined in detail in **chapter 4**.

Development from the egg to an adult can be interrupted for a certain period, known as **dormancy**, when environmental conditions are

ORDER	LARVA	ADULT
Diptera: mosquitoes	aquatic larvae feed on algae and microorganisms chewing mouthparts	adult female mosquitoes feed on blood of vertebrates and invertebrates piercing-sucking mouthparts
horseflies	larvae feed on various solid food chewing mouthparts	adults cut open cuticle of prey and suck body juices cutting-sponging mouthparts
Hymenoptera: wasps	larvae feed on plant material or animals chewing mouthparts	adults feed on liquid food (nectar) and solid food chewing-lapping mouthparts
Lepidoptera: butterflies/moths	larvae feed on vegetation chewing mouthparts	adults drink nectar or water mouthparts of siphoning-tube type

Box 2-2: Change in mouthparts during the holometabolous development of selected insect groups

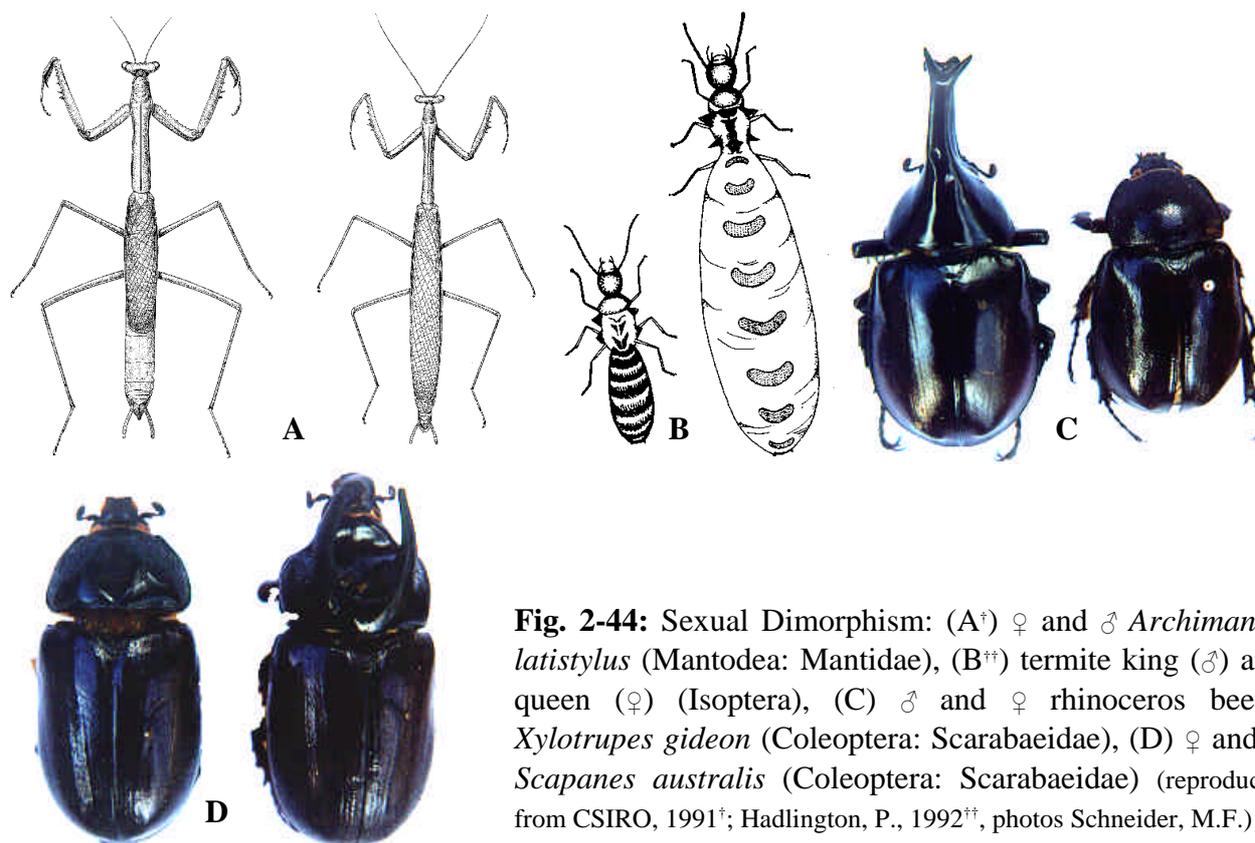


Fig. 2-44: Sexual Dimorphism: (A⁺) ♀ and ♂ *Archimantis latistylus* (Mantodea: Mantidae), (B⁺⁺) termite king (♂) and queen (♀) (Isoptera), (C) ♂ and ♀ rhinoceros beetle *Xylotrupes gideon* (Coleoptera: Scarabaeidae), (D) ♀ and ♂ *Scapanes australis* (Coleoptera: Scarabaeidae) (reproduced from CSIRO, 1991[†]; Hadlington, P., 1992^{††}, photos Schneider, M.F.)

unsuitable. This is common in temperate areas during winter. It would not make sense for insects to develop because it might be too cold and foodplants be absent. Dormancy can also occur during drought, as could be observed during the prolonged dry-spell in PNG in 1997, when most of the insect diversity vanished. Once the rain started at the end of 1997, nature woke up again providing the necessary food and within a few weeks many insect species arose from dormancy, too.

Quiescence is the simplest form of dormancy. It is a direct response to adverse environmental conditions, halting or slowing down the development which resumes immediately, once the conditions become more favourable.

In contrast, **diapause** is arrested development, which persists for some time, even if suitable conditions are prevailing. Diapause is often associated with physiological changes and the resumption of development requires internal stimuli. **Obligatory** diapause occurs during a fixed time of the year in **univoltine** insects and is usually genetically controlled. Insects with one generation per year need to extend their

short life cycle in order to avoid a second generation that would conflict with unsuitable conditions. An optional **facultative** diapause can be found in **bivoltine** or **multivoltine** insects with two or more generations per year. Only those generations that have to sustain adverse conditions are subject to diapause.

Various abiotic and biotic factors as well as internal physiological stimuli like **Diapause Hormone** trigger diapause. Diapause can last from days to months or up to seventeen years as in the case of the northern American periodical cicada *Magicicada septemdecim*. Any stage of the life cycle can undergo diapause, but egg and pupal diapause are the commonest. These stages are resting stages with little activity thus increasing the chances of survival.

Diapause allows insects to adapt their life cycles to the seasonal rhythm of the environment. Thus, active stages, that are not able to escape from unsuitable conditions by means of migration, are present only during favourable conditions. Diapause also enables the synchronisation of adult emergence for reproduction or migration.

The time required to complete one full life cycle varies from several days for a few minute insects to several weeks for the majority of insects in the tropics up to several months for larger insects or insects of temperate areas. However, diapause or quiescence might markedly extend the life cycle of a particular species. The information about the life history of a particular pest species as well as the duration of its stages is most valuable and even a requirement for the prediction of outbreaks and effective control strategies. This is further outlined in **chapter 4.7**.

Further reading:

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- Roberts, M.B.V. (1985⁴): Biology - A Functional Approach; ELBS; Walton-o.-T.; UK
- Ross, H.H. et al. (1982⁴): A Textbook of Entomology; Wiley; New York; USA
- de la Torre-Bueno, J.R. (1989²): The Torre-Bueno Glossary of Entomology; New York Entomological Society in Cooperation with the American Museum of Natural History; New York; USA



Fig. 2-45: “Poem Case”, by Dodd, F.P. The words are spelled out in tiny pyralid moths while the signature is in metallic green beetles (reproduced from Monteith, G., 1991)