* Insects have an open blood system with the blood occupying the general body cavity which is thus known as a **haemocoel**. Blood is circulated mainly by the activity of a contractile longitudinal vessel (called the **dorsal vessel**) which opens into the haemocoel and which usually lies in a dorsal **pericardial sinus**, cut off by a **dorsal diaphragm** from the **perivisceral sinus** which contains the viscera. Sometimes there is also a **ventral diaphragm** above the nerve cord which cuts off a ventral **perineural sinus** from the perivisceral sinus. The perineural sinus is normally only a small part of the haemocoel, but in Ichneumonidae it may form half the body cavity because the sterna, to which the ventral diaphragm is attached, are extended upwards.

THE DORSAL VESSEL

* The dorsal vessel runs nearly the entire length of the body and it runs along the dorsal midline just below the terga. Anteriorly, it leaves the dorsal wall and is more closely associated with the alimentary canal, passing under the cerebral ganglion just above the oesophagous. The dorsal vessel is divided into 2 regions: a posterior **heart**, and an anterior **aorta**. The dorsal vessel is open ended anteriorly and closed ended posteriorly, except in Ephemeroptera nymphs in which the posterior end divides into 3 branches which enter the cerci and the median caudal filament. The wall of the dorsal vessel is contractile and consists of a single layer of cells in which circular or spiral muscle fibrils are differentiated. In the Heteroptera, longitudinal muscle strands are also present, especially around the aorta. A network of tracheoles is often present, especially around the posterior part of the heart.

* **Heart** - The heart is usually restricted to the abdomen but may extend as far anteriorly as the prothorax as in some Dictyoptera. The heart has the wall of the vessel perforated by **incurrent ostia** and sometimes **excurrent ostia**. In some insects (orthopteroids) the heart has the appearance of chambers at the points where the **ostia** pierce the wall of the heart. These enlarged chambers are called **ampullae** (sing. ampulla). The ampullae are more prominent in the thorax. In some insects (Odonata and some Diptera-*Tipula*), the heart is divided into chambers by valves in front of each pair of incurrent ostia. The heart may be directly bound to the dorsal body wall of the insect or it may be suspended from it by elastic filaments.

* **Incurrent ostia** - The incurrent ostia are vertical slit-like openings occurring laterally in the heart wall. There may be 9 pairs of incurrent ostia in the abdomen and up to 3 pairs in the thorax. All 12 pairs are present in the Dictyoptera, but there are only 5 pairs in the aculeate Hymenoptera and only 3 pairs in *Musca* (Diptera). In some Mallophaga, Diptera, and Heteroptera there may only be 2-3 pairs of ostia and the heart is restricted to the posterior abdominal segments. The anterior and posterior lips of the ostia are reflexed into the heart so that they form a valve permitting the flow of blood into the heart at **diastole** (expansion of heart), but preventing its outward passage at **systole** (contraction of heart). During diastole the lips are forced apart by the inflowing blood. When diastole is complete the lips are forced together by the pressure of the blood in the heart and they remain closed throughout systole. Towards the end of systole the valves tend to become evaginated by the pressure, but are prevented from turning completely inside out by a unicellular thread attached to the inside of the heart. In *Bombyx* (Lepidoptera) only the posterior lip of each ostium is extended as a flap within the heart. During systole this is pressed against the wall of the heart so that the excape of blood is prevented.

* **Excurrent ostia** - The excurrent ostia are usually paired ventrolateral openings in the wall of the heart without any internal valve. The number of excurrent ostia varies, but some grasshoppers have 2 thoracic and 5 abdominal pairs. Externally each opening is surrounded by a papilla of spongiform multinucleate cells which expands when the heart contracts, so that blood passes out, and contracts when the heart relaxes, so that the entry of blood is prevented. There are also unpaired excurrent ostia in the heart of Plecoptera and Embioptera.

* **Segmental vessels** - Most Dictyoptera do not have excurrent ostia, but there are definite segmental vessels by which the blood leaves the heart. In the cockroaches there are 2 thoracic and 4 abdominal vessels, but only the abdominal vessels are present in the mantids. They originate from the heart between the aliform

muscles and branch distally and disappear into the fat tissue. There are groups of loosely packed cells at the base of each vessel which functions as a valve only permitting the outward flow of blood. The walls of the vessels are non-musculated, but there is some evidence that they do contract independently from the heart. It may be that the cells at the base of the vessel may contract and cause a wave of contraction to travel down the vessel.

* **Phagocytic organs** - In the anterior part of the abdomen in some Orthoptera are found phagocytic organs which are flattened triangular sacs opening ventrolaterally from the heart by narrow connections, at which are excurrent valves, and then they fan out between the aliform muscles. There may be 2 to 4 pairs of phagocytic organs. The ventral wall of these organs is formed by the dorsal diaphragm, the dorsal wall by the phagocytic cells which are multinucleate and occupy part of the lumen of each sac. These organs seem to act as filters removing dyes and particles from the blood which is forced into while the blood is presumed to percolate back through the dorsal diaphragm.

* **Aorta** - The dorsal vessel continues anteriorly from the heart in an undifferentiated tube which lacks ostia. This tube is called the **aorta**. In some insects (Odonata, Orthoptera, Coleoptera, and Lepidoptera) there may be diverticula extending dorsally from the aorta. These diverticula are often connected with the **pulsatile organs** which are concerned with blood circulation through the wings. Anteriorly the aorta is open ended but may take different forms such as an open gutter (Orthoptera), or an abrupt ending (most insects).

ALIFORM MUSCLES AND THE DORSAL DIAPHRAGM

* Closely associated with the heart are the aliform or alary muscles. These stretch from one side of the body to the other just below the heart. Usually they fan out from a restricted point of attachment from the tergum, the muscles of each side meeting in a broad zone at the midline. In some Orthoptera the origin of the muscles is also broad. In most Orthoptera, only the proximal part near the point of attachment is contractile. The rest of the muscle being made up of mainly connective tissue. Some of the connective tissue forms a plexus which continues to the heart wall, but in some insects (some Diptera larvae) the aliform muscles insert directly into the heart wall rather than meeting beneath it. Orthopteroids may have 10 abdominal and 2 thoracic pairs of aliform muscles, but this number is reduced in most other insects. Some Heteroptera have only 4-7 pairs.

* The aliform muscles form an integral part of the dorsal diaphragm which spreads between them as a fenestrated (**fenestrae** are small openings in the membrane) connective tissue membrane. It is usually incomplete laterally so that the pericardial sinus is broadly continuous with the perivisceral sinus in this region. The lateral limits are often indefinite and are determined by the presence of muscles or tracheae or the origins of the aliform muscles.

VENTRAL DIAPHRAGM

* The ventral diaphragm is a horizontal septum just above the nerve cord cutting off the perineural sinus from the perivisceral sinus. It is unusual in the Lepidoptera in that the nerve cord is bound to its ventral surface by connective tissue. The ventral diaphragm is connected laterally to the sternum usually only at one point per segment leaving broad gaps along its margins where the perineural and perivisceral sinuses are continuous. In many orders it is restricted to the abdomen, but in the Orthoptera it is also present in the thorax. Posteriorly it does not extend beyond the posterior end of the nerve cord.

ACCESSORY PULSATILE ORGANS

* Sometimes there are present pulsatile organs which aid in the movement of the blood. For example there is often an organ in the mesothorax and/or the metathorax which helps move the blood through the wings. In some Lepidoptera the dorsal vessel itself loops up to the dorsal surface of the thorax and becomes the pulsatile organ.

* Orthoptera and probably many other insects have a small ampulla at the base of each antenna. This opens to the haemocoel by a small valve and extends as a vessel into the antenna. When the ampulla expands blood flows into it; when it contracts blood is forced into the antenna. Other pulsating organs occur in the legs of Heteroptera.

HAEMOLYMPH

* The blood or haemolymph of insects consists of a **fluid plasma** in which **nucleated cells** are suspended. Several different types of blood cells occur and the number in circulation varies considerably. The haemolymph is usually colorless but is sometimes yellow or green. Some midges (blood worms) have hemoglobin in the blood and so the blood appears red.

HAEMOCYTES

* **Types of haemocytes** - types 1-4 occur in most insects. (note that low pH = acidic, and high pH = basic [alkaline])
    1. Prohaemocytes - small rounded cells with relatively large nuclei and intensely basophilic cytoplasm. They divide at frequent intervals and give rise to other types of cells.
    2. Plasmatocytes - frequently are the most abundant cell type. They are variable in form, phagocytic and with a basophilic cytoplasm.
    3. Granular haematocytes - are also phagocytic, but are characterized by the possession of acidophilic granules in the cytoplasm.
    4. Cystocytes - have a small, sharply defined nucleus and a pale, hyaline cytoplasm containing scattered black granules. The cystocytes are probably specialized granular haematocytes.
    5. Oenocytoids - found in Coleoptera, Lepidoptera, and some Diptera and some Heteroptera. They are usually large, thick, basophilic cells containing canaliculi or strands of granules or crystals.
    6. Spherule cells - occurs in Lepidoptera and Diptera. They are round or oval cells with large, non-refringent, usually acidophilic inclusions filling the whole cell.
    7. Adipohaemocytes - found in Lepidoptera and Diptera. They are characterized by refringent (or refractive) fat droplets and other inclusions.

    * It is not clear if these different types of haemocytes are different stages in the development of individual cells, but it seems probable that most of them are derived independently from prohaemocytes.

* **Functions of haemocytes**
    1. Phagocytosis - this is the most common function - eating foreign particles, micro-organisms, and tissue debris. Many cells are capable of phagocytosis, but probably the plasmatocytes are most important.
    2. Encapsulation - Particles such as metazoan parasites which are too large to phagocytose are encapsulated. The haemocytes congregate around the parasite and become flattened. More adhere to the outside so that the capsule becomes smooth and consolidated.
    3. Secretion and metabolism - Haemocytes may be concerned in the formation of connective tissue. These come from mucopolysaccharides that are secreted from the haemocytes. Some haemocytes may be concerned with the formation of fat body and are concerned with intermediate metabolism. This is true of the spherule cells.
    4. Wound healing and coagulation - Damaged tissues are phagocytosed and the plasmatocytes extend processes which join those of other cells to form a cellular network. The plasma may coagulate in this network so that the wound is effectively plugged until the epidermis regenerates.

PLASMA

* **Functions of the plasma**
    1. Transport of substances around the body - this is the primarily function. Nutritive substances are transported from the alimentary canal and storage tissues to the sites where they are to be metabolized. Excretory products are transported from where they are produced to the Malpighian tubules. Hormones are transported from the endocrine glands to their sites of action.

2. Storage of substances - such as sugars and proteins.
3. Storage of water - Water acts as a reservoir for the maintenance of tissue fluids. The hydrostatic pressure of the haemolymph is important in the movements of soft-bodied larvae, in expansion after molting, and in the eversion of various organs (penis and osmeterium).
4. Reflex bleeding - this also results from an increase in hydrostatic pressure. Plasma is forced out through weak spots or pores in the cuticle. The blood in these insects always contain some caustic or repellant substance so this is presumed to be a defensive mechanism.

CIRCULATION OF THE HAEMOLYMPH

* In normal circulation the blood is pumped forwards through the heart at systole, passing out of the heart via the excurrent ostia and, anteriorly, from the aorta. The blood driven forward by the heart increases the pressure anteriorly in the perivisceral sinus so that in this sinus the blood tends to flow posteriorly along a pressure gradient. Blood percolates down to the perineural sinus where it is agitated by movements of the ventral diaphragm which assist the blood flow to the nerve cord and possibly produce a backward flow of blood. The dorsal diaphragm is usually convex above so that contraction of the alary muscles tends to flatten it. This flattening increases the volume of the pericardial sinus at the expense of the perivisceral sinus so that this causes a flow of blood up into the pericardial sinus, and then into the heart at diastole through the incurrent ostia.

* In general the flow through the wings is outward through the anterior veins and then inward through the posterior veins. The passage from anterior veins to posterior veins is via the cross veins. The blood flows from the posterior veins back into the body via the axillary cord.

* The pulsatile organs help the flow of blood through the antennae and in the Heteroptera the legs. Most insects have a longitudinal septa dividing the legs into an anterior and a posterior channel. In most insects the blood flows outward through the posterior channel and inward through the anterior channel.

* The flow of blood can be reversed in some insects (Cockroaches).