* Gaseous exchange in insects is carried on through a system of internal tubes, the **tracheae**, the finer branches of which extend to all parts of the body and may become functionally intracellular in muscle fibers. Thus oxygen is carried directly to its sites of utilization and the blood is not concerned with gas transport. The tracheae open to the outside of the body through segmental pores called **spiracles**, which generally have some closing mechanism which keeps water loss at a minimum. The spiracles open in response to low internal concentration of oxygen or a high concentration of carbon dioxide in the tissues.

* Diffusion alone can account for the gaseous requirements of most insects at rest, but larger insects and active insects require a better system - the tracheal system.

THE TRACHEAL SYSTEM

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

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

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

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

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

SPIRACLES

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

* **Number and distribution of spiracles** - With the exception of some Diplura, the largest number of spiracles found in insects is 10 pairs, 2 thoracic and 8 abdominal, and the respiratory system can be classified on the basis of the number and distribution of the functional spiracles:
    1. **Polypneustic** - at least 8 functional spiracles on each side:
        a. **Holopneustic** - 10 spiracles - 1 mesothoracic, 1 metathoracic, 8 abdominal - as in bibionid larvae.
        b. **Peripneustic** - 9 spiracles - 1 mesothoracic, 8 abdominal - as in cecidomyid larvae.
        c. **Hemipneustic** - 8 spiracles - 1 mesothoracic, 7 abdominal - as in mycetophilid larvae.
    2. **Oligopneustic** - 1 or 2 functional spiracles on each side:
        a. **Amphipneustic** - 2 spiracles - 1 mesothoracic, 1 post-abdominal - as in psychodid larvae.
        b. **Metapneustic** - 1 spiracle - 1 post-abdominal - as in culicid larvae.
        c. **Propneustic** - 1 spiracle - 1 mesothoracic - as in dipterous pupae.
    3. **Apneustic** - no functional spiracles - as in chironomid larvae.

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

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

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

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

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

CUTANEOUS RESPIRATION

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

OTHER FUNCTIONS OF THE TRACHEAL SYSTEM

* The whole tracheal system, and in particular the air-sacs, lowers the specific gravity of the insect. In aquatic insects, but not in terrestrial ones, it also gives some degree of buoyancy which can be adjusted. Expansion of the tracheal system may assist in inflation of the insect after a molt. Some air-sacs near the flight muscles

are thought to aid in cooling of the muscles during periods of high activity. There is an air chamber in cicadas that functions as a resonating chamber to help amplify its call.

RESPIRATION IN AQUATIC INSECTS

* Aquatic insects obtain oxygen from the air or from air dissolved in the water. Most get their oxygen directly from the air. This usually requires periodic visits to the surface. A few insects, however, maintain a semi-permanent connection with the air via a long respiratory siphon or through the aerenchyma of certain aquatic plants. Insects returning to the surface face 2 main problems. First they must be able to break the surface film of the water, and secondly they must be able to keep the water from entering the spiracles once they re-enter the water. Respiration by aquatic insects usually requires one of the following modifications:
    1. **tracheal gills** - evaginated trachea or tracheoles. Found in immatures (Stoneflies, Mayflies, some Odonata).
    2. **rectal gills** - Found in Odonata. Inside the rectum there are 5 tracheoles, water is taken into the rectum, the oxygen is removed, and then the water is expelled.
    3. **spiracular gills** - Found in aquatic Diptera. Often are insects that are associated with streams that periodically dry up. When in water they function as gills. If stream dries up part of the gills break off leaving a hole so air can enter directly.
    4. **respiratory tubes** - Found in Nepidae (water scorpions). Simply is a siphon or respiratory tube.
    5. **post-abdominal siphon** - found in mosquitoes. This is a posterior sharp siphon that is used to pierce the plant tissue to obtain oxygen.
    6. **air bubble** - Found in aquatic Hemiptera and Coleoptera. The insect captures a bubble of air at surface and carries it below surface and use it to breathe. Sometimes the oxygen diffuses from the water directly into the air bubble.
    7. **plastron respiration** - This is called a hydrofuge and consists of special hairs which trap a bubble. The hairs prevent the bubble from collapsing. The insect can stay underwater with 1 bubble for up to 4 months.

RESPIRATION IN ENDOPARASITIC INSECTS

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

HAEMOGLOBIN

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