15

Gas Exchange

1. Introduction

In all organisms gas exchange, the supply of oxygen to and removal of carbon dioxide from cells, depends ultimately on the rate at which these gases diffuse in the dissolved state. The diffusion rate is proportional to (1) the surface area over which diffusion is occurring and (2) the diffusion gradient (concentration difference of the diffusing material between the two points under consideration divided by the distance between the two points). Diffusion alone, therefore, as a means of obtaining oxygen or excreting carbon dioxide can be employed only by small organisms whose surface area/volume ratio is high (i.e., where all cells are relatively close to the surface of the body) and organisms whose metabolic rate is low. Organisms that are larger and/or have a high metabolic rate must increase the rate at which gases move between the environment and the body tissues by improving (1) and/or (2) above. In other words, specialized respiratory structures with large surface areas and/or transport systems that bring large quantities of the gas closer to the site of use or disposal (thereby improving the diffusion gradient) have been developed. For most terrestrial animals prevention of desiccation is another important problem, and this has had a major influence on the development of their respiratory surfaces through which considerable loss of water might occur. Typically, respiratory surfaces of terrestrial animals are formed as invaginated structures within the body so that evaporative water loss is greatly reduced.

In insects the tracheal system, a series of gas-filled tubes derived from the integument, has evolved to cope with gas exchange. Terminally the tubes are much branched, forming tracheoles that provide an enormous surface area over which diffusion can occur. Furthermore, tracheoles are so numerous that gaseous oxygen readily reaches most parts of the body, and, equally, carbon dioxide easily diffuses out of the tissues. Thus, in most insects, in contrast to many other animals, the circulatory system is unimportant in gas transport. Because they are in the gaseous state within the tracheal system, oxygen and carbon dioxide diffuse rapidly between the tissues and site of uptake or release, respectively, on the body surface. Oxygen, for example, diffuses 3 million times faster in air than in water (Mill, 1972). Again, because the system is gas-filled, much larger quantities of oxygen can reach the tissues in a given time. (Air has about 25 times more oxygen per unit volume than water.)

The eminent suitability of the tracheal system for gas exchange is illustrated by the fact that, for most small insects and many large insects at rest, simple diffusion of gases in/out

of the tracheal system entirely satisfies their requirements (but see Section 3.3). In large, active insects the gradient over which diffusion occurs is increased by means of ventilation; that is, air is actively pumped through the tracheal system.

2. Organization and Structure of the Tracheal System

A tracheal system is present in all Insecta and in other hexapods with the exception of the Protura and many Collembola. It arises during embryogenesis as a series of segmental invaginations of the integument. Up to 12 (3 thoracic and 9 abdominal) pairs of spiracles may be seen in embryos, though this number is always reduced prior to hatching, and further reduction may occur in endopterygotes during metamorphosis. Various terms are used to describe the number of pairs of functional spiracles, for example, holopneustic (10 pairs, located on the mesothorax and metathorax and 8 abdominal segments), amphipneustic (2 pairs, on the mesothorax and at the tip of the abdomen), and apneustic (no functional spiracles). The last condition is common in aquatic larvae, which are said, therefore, to have a closed tracheal system (Section 4.1).

The proportion of the body filled by the tracheal system varies widely, both among species and within the same individual throughout a stadium. In active insects whose tracheal system includes air sacs (see below) the tracheal system occupies a greater fraction of the body than in less active species. Further, in the former, the volume of the tracheal system may decrease dramatically during a stadium (e.g., in *Locusta* from 48% to 3%) as the air sacs become occluded by the increased hemolymph pressure that results from tissue growth. After ecdysis, when body volume has increased (Chapter 11, Section 3.2), the tracheal system expands because of the lowered hemolymph pressure.

2.1. Tracheae and Tracheoles

In apterygotes other than lepismatid Zygentoma, the tracheae that run from each spiracle do not anastomose either with those from adjacent segments or with those derived from the spiracle on the opposite side. In the Lepismatidae and Pterygota both longitudinal and transverse anastomoses occur, and, though minor variations can be seen, the resultant pattern of the tracheal system is often characteristic for a particular order or family. Generally, a pair of large-diameter, longitudinal tracheae (the lateral trunks) run along the length of an insect just internal to the spiracles. Other longitudinal trunks are associated with the heart, gut, and ventral nerve cord. Interconnecting the longitudinal tracheae are transverse commissures, usually one dorsal and another ventral, in each segment (Figure 15.1). Parts of the tracheal system, for example, that of the pterothorax, may be effectively isolated from the rest of the system by reduction of the diameter or occlusion of certain longitudinal trunks. This arrangement is associated with the use of autoventilation as a means of improving the supply of oxygen to wing muscles during flight (Section 3.3). Also, tracheae are often dilated to form large thin-walled air sacs that have an important role in ventilation (Section 3.3) and other functions.

Numerous smaller tracheae branch off the main tracts and undergo progressive subdivision until at a diameter of about 2–5 μm they form a number of fine branches each 1 μm or less across known as tracheoles. Tracheoles are intracellular, being enclosed within a very thin layer of cytoplasm from the tracheoblast (tracheal end cell) (Figure 15.2), and ramify throughout most tissues of the body. They are especially abundant in metabolically active tissues. Thus, in flight muscles, fat body, and testes, for example, tracheoles indent