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Muscles and Locomotion

1. Introduction

The ability to move is a characteristic of living animals and facilitates distribution, food procurement, location of a mate or egg-laying site, and avoidance of unsuitable conditions. Insects, largely through their ability to fly when adult, are among the most mobile and widely distributed of animals. Development of this ability early in the evolution of the class has made the Insecta the most diverse and successful animal group (Chapter 2, Section 3.1). However, flight is only one method of locomotion employed by insects. Terrestrial species may walk, jump, or crawl over the substrate, or burrow within it. Aquatic forms can swim in a variety of ways or run on the water surface.

In their locomotory movements, insects conform to normal dynamic and mechanical principles. However, their generally small size and light weight have led to the development of some unique structural, physiological, and biochemical features in their locomotory systems.

2. Muscles

Essentially, the structure and contractile mechanism of insect muscles are comparable to those of vertebrate skeletal (cross-striated) muscle; that is, there are no muscles in insects of the smooth (non-striated) type. Within muscle cells, the contractile elements actin and myosin have been identified, and Huxley's sliding filament theory of muscle contraction applies. Though insect muscles are always cross-striated, there is considerable variation in their structure, biochemistry, and neural control, in accord with specific functions.

Because of their small size and the variable composition of the hemolymph of insects, the neuromuscular system has some unique features (Hoyle, 1974). Being small, an insect has a limited space for muscles which are, accordingly, reduced in size. Though this is achieved to some extent by a decrease in the size of individual cells (fibers), the principal change has been a decline in the number of fibers per muscle such that some insect muscles comprise only one or two cells. Thus, to achieve a graded muscle contraction, each fiber must be capable of a variable response, in contrast to the vertebrate situation where graded muscle responses result in part from stimulation of a varied number of fibers. Similarly, the volume of nervous tissue is limited, so that there are few motor neurons for the control of muscle

contraction. The hemolymph surrounding muscles may contain high concentrations of ions (especially divalent ions such as Mg^{2+}) (Chapter 17, Section 4.1.1) that could interfere with impulse transmission at synapses and neuromuscular junctions. That this does not occur is the result of the evolution of a myelin sheath that covers ganglia, nerves, and neuromuscular junctions.

2.1. Structure

Insect muscles can be arranged in two categories: (1) skeletal muscles whose function is to move one part of the skeleton in relation to another, the two parts being separated by a joint of some kind, and (2) visceral muscles, which form layers of tissue enveloping internal organs such as the heart, gut, and reproductive tract.

Attachment of a muscle to the integument must take into account the fact that periodically the remains of the old cuticle are shed; therefore, an insertion must be able to break and re-form easily. As Figure 14.1 indicates, a muscle terminates at the basal lamina lying beneath the epidermis. The muscle cells and epidermal cells interdigitate, increasing the surface area for attachment by about 10 times, and desmosomes occur at intervals, replacing the basal lamina. Attachment of a muscle cell to the rigid cuticle is achieved through large numbers of parallel microtubules (called "tonofibrillae" by earlier authors). Distally, the epidermal cell membrane is invaginated, forming numbers of conical hemidesmosomes on which the microtubules terminate. Running distad from each hemidesmosome is one, rarely two, muscle attachment fibers (= tonofibrils). Each fiber passes along a pore canal

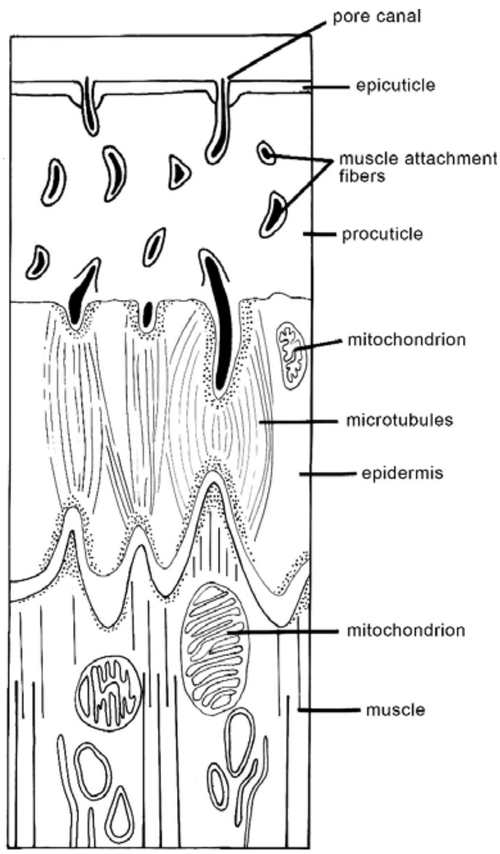

FIGURE 14.1. Muscle insertion. [After A. C. Neville, 1975, *Biology of the Arthropod Cuticle.* By permission of Springer-Verlag, New York.]