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The Integument

1. Introduction

The integument of insects (and other arthropods) comprises the basal lamina, epidermis, and cuticle. It is often thought of as the "skin" of an insect but it has many other functions (Locke, 1974). Not only does it provide physical protection for internal organs but, because of its rigidity, it serves as a skeleton to which muscles can be attached. It also reduces water loss to a very low level in most Insecta, a feature that has been of great significance in the evolution of this predominantly terrestrial class. In addition to these primary functions, the cuticular component of the integument performs a number of secondary duties. It acts as a metabolic reserve, to be used cyclically to construct the next stage, or during periods of great metabolic activity or starvation. It prevents entry of foreign material, both living and nonliving, into an insect. In many insects the waxy outer layer serves as a repository for contact sex pheromones (Chapter 13, Section 4.1.1). The color of insects is also a function of the integument, especially the cuticular component.

The integument is not a uniform structure. On the contrary, both its cellular and acellular components may be differentiated in a variety of ways to suit an insect's needs. Epidermal cells may form specialized glands that produce components of the cuticle or may develop into particular parts of sense organs. The cuticle itself is variously differentiated according to the function it is required to perform. Where muscles are attached or where abrasion may occur it is thick and rigid; at points of articulation it is flexible and elastic; over some sensory structures it may be extremely thin.

2. Structure

The innermost component of the integument (Figure 11.1) is the basal lamina, an amorphous but selectively porous acellular layer that is attached by hemidesmosomes to the epidermal cells. It is up to 0.5 μm thick and is produced mainly by the epidermis, though there are reports that hemocytes also participate. The chemical nature of the basal lamina is poorly understood though neutral mucopolysaccharide, glycoproteins, and collagen, similar to that of vertebrates, have been identified.

The epidermis (hypodermis) is a more or less continuous sheet of tissue, one cell thick, responsible for secreting the bulk of the cuticle. During periods of inactivity, its

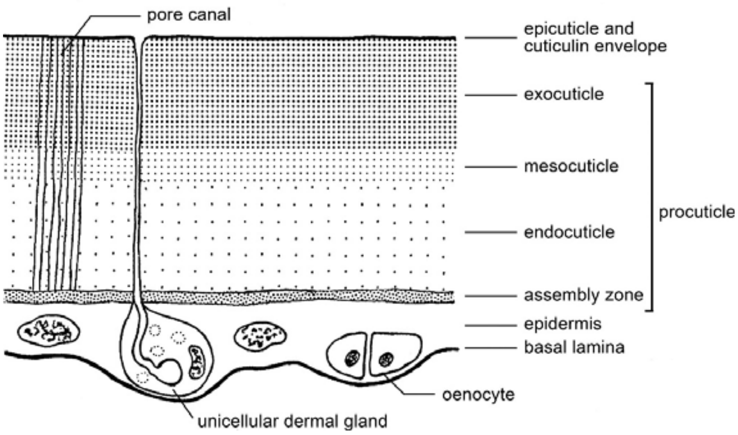

FIGURE 11.1. Diagrammatic cross-section of mature integument.

cells are flattened and intercellular boundaries are indistinct. When active, the cells are more or less cuboidal, and their plasma membranes are readily apparent; one to several nucleoli, extensive rough endoplasmic reticulum, and many Golgi complexes are evident (Locke, 1991, 1998). A characteristic feature of the apical (cuticle-facing) surface of epidermal cells are the plasma membrane plaques, specialized regions of the plasma membrane at the tips of fingerlike microvilli, from which the cuticulin envelope and new chitin fibers arise (Section 3.1). Electron microscopy has shown that, at metamorphosis, the epidermal cells develop basal processes ("feet") which can extend to become connected with the basal lamina and with other epidermal cells. When the feet shorten, the basal lamina is buckled and rearrangement of cells occurs, resulting in a change in the insect's shape, for example, from a long, thin caterpillar to a short, fat pupa (Locke, 1991, 1998). Epidermal cells also possess the ability to develop various forms of cytoskeletal extensions which can be used, for example, to draw tracheoles closer to the cell for increased oxygen supply, or to maintain intercellular contact as the cells migrate during wound healing and changes in body shape. The density of cells in a particular area varies, following a sequence that can be correlated with the molting cycle. The cells often contain granules of a reddish-brown pigment, insectorubin, which in some insects contributes significantly to their color. However, in most insects color is produced by the cuticle (Section 4.3).

Epidermal cells may be differentiated into sense organs or specialized glandular cells. Oenocytes are large, ductless, often polyploid cells, up to 100 μm in diameter. They occur in pairs or small groups and the cells of each group may be derived from one original epidermal cell. Usually they move to the hemocoelic face of the basal lamina, though in some insects they form clusters in the hemocoel or migrate and reassemble within the fat body. Oenocytes show signs of secretory activity that can be correlated with the molting cycle, and, on the basis of certain staining reactions, it has been suggested that they produce the lipoprotein component of epicuticle. In addition, ultrastructural and biochemical studies have led to the proposal that these cells produce ecdysone (Locke, 1969; Romer, 1991). They also synthesize components of the cuticular wax, including some contact sex pheromones (Blomquist and Dillwith, 1985; Schal *et al.*, 1998). Dermal glands of various types are also differentiated. In their simplest form the glands are unicellular and have a long duct that penetrates the cuticle to the exterior. More commonly, they are composed of several cells.