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Reviews

The physiology and biology of spinning in *Bombyx mori*

I. Introduction

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Certain species of Insecta and Arachnida spin a number of different types of silk for a variety of specialized purposes such as the fabrication of a cocoon and the construction of a nest. The amino acid compositions of various fibroins from more than 70 species of the arthropods have been compared. All those fibroins examined so far are characterized by high proportions of the simple amino acids, glycine, alanine and serine. Among Insecta, *Bombyx mori,* a species of the subfamily Bombycidae, is the most familiar and the most extensively studied. Therefore, when the term silkworm is used without qualification in this review, the reader may presume that it is *Bombyx mori* that is referred to.

Recently, the silkworm has become more and more attractive for basic research in the field of biological sciences as a model system in eukaryotes. Processes of biosynthesis and spinning of silk proteins in the silk glands of the silkworm are particularly interesting from the standpoint of the mechanism of selective gene expression in a highly differentiated type of cells. The silkworms have been reared with only mulberry leaves from olden times. This monophagous character has hampered a wide use of the silkworm as a laboratory tool. Recently, however, artificial diets for silkworm rearing have been devised and greatly improved. At present, there are only small differences in the rates of growth and development of larvae reared on mulberry leaves and artificial diets. Thus, physiological and biochemical research performed with the silkworm is now gradually increasing in the world. Artificial diets are commercially available from several feed companies in Japan.

The silk gland of the larva of *Bombyx mori* is divided into 3 parts according to their secretory functions (chapter II). The posterior silk gland synthesizes exclusively silk fibroin, a main component of the silk proteins, and secretes it into the lumen of the gland. The fibroin excreted is transferred by peristalsis into the middle silk gland, in which it is stored until required for spinning. In the middle silk gland, sericin, another silk protein, is secreted into the gland lumen and coats the fibroin granules in the lumen. The anterior silk gland is a narrow duct and it plays an important role in the processes of spinning the silk proteins.

The silk glands are derived from the ectoderm and begin development as paired invaginations in the labial segments. The cell division in the gland is limited to the embryonic stages and no cell division takes place during the entire larval stage. The number of cell in a pair of silk glands at the larval stage is approximately 600 in the anterior, 500 in the middle, and 1000 in the posterior part.

During the larval development the cells in the glands continue to increase in size as a result of repeated replication of chromosomes. The largest cells, which are located in the midsection of the middle gland, reach dimensions of about 1×4 mm. The DNA content of each cell in the posterior glands increases about 200,000-fold over that expected for diploid cells, leading to a highly complicated ramification of nuclei.

The process of spinning in a narrow sense is not merely an excretion of the silk proteins stored in the silk glands; it is a fairly complicated physico-chemical phenomenon. Aqueous silk in the anterior division of the silk gland turns to fiber through the combined forces of drawing by the motion of a silkworm's head and ejection from inside through the spinneret. The spinning speed ranges from 0.4 to 1.5 cm/sec. This limited value seem critical for completing the spinning of whole silk materials without a break. In *Bombyx mori,* the silk fiber reachs about 1000–1500 m in length with a diameter of about 2 μm. The physicochemical aspects in the fiber spinning process will be discussed in chapter III in this review.

A considerable number of molecular biological studies on the biosynthesis of silk proteins in the silk glands, most of them on fibroin synthesis, have been accumulated during the last 2 decades. The metabolic activity of the silk gland cells of the *Bombyx mori* at the 5th instar is highly and specifically directed to the synthesis of silk proteins. This feature makes it rather simple for us to establish a cell-free system for protein synthesis, isolation of messenger RNA of silk proteins, and genetic studies on the silk protein genes. Recently it has become more likely that silk fibroin is composed of large and small subunits, and that the small subunit as well as the large subunit is synthesized in the posterior silk gland. However, almost all studies performed on the fibroin synthesis have been done so far without considering this subunit structure of the fibroin. The subunit structure of the fibroin molecule and its relation to fibroin synthesis will be discussed in some detail in section IV.

Insect hormones have been a subject of deep and continuing interest in biology. One of the reasons why physiologists as well as biochemists are interested in insect hormones is that the research worker can deal with the basic nature of the chief functions of the insect organism in a physiological manner, i.e., without disturbing any of the important life processes, and can thus understand the nature of the functions more profoundly. This is also the basis of the great relevance of insect hormone research to general biology. Not only the academic importance of insect hormone research, but also its practical applications to sericultural industry have become increasingly obvious in recent years. Thus hormone research affects the future practice of the rearing of the silkworm and the improvement of appropriate techniques.

In *Bombyx mori,* 4 hormones, that is, brain, juvenile, molting and diapause hormones, are most extensively and profoundly studied. The program of the synthesis of silk protein in the silk glands and the spinning of the protein synthesized is completely under the control of hormones. The brain hormone of *B. mori* consists of several kinds of proteins. They are mainly released from the corpus allatum into the blood stream and stimulate the activity of the prothoracic gland to secrete ecdysteroids. The ecdysteroids play an important role in the promotion and maintenance of fibroin synthesis. Although the ecdysteroid content in the hemolymph of the silkworm is low at the first half of the 5th instar, it increases gradually over the 3 days and reaches a maximum, at which time the activity of synthesis of the silk protein is also the highest.

In contrast to the molting hormone, the juvenile hormone prevents larval development. Treatment of the silkworm with juvenile hormone during the first half of the last instar induces a prolongation of the instar, that is, a delay in the spinning of the cocoon, accompanied by the increase of silk secretion. A later treatment interferes with pupal metamorphosis and leads to an extra larval molt. One of the primary effects of the juvenile hormone-treatment seems to be the suppression of the RNA synthesis in the silk glands, which is known to take place most actively during the first half of the last instar. These hormonal controls and sterol metabolism in the silkworm will be discussed in sections V and VI.

The reader is referred to a number of texts, chapters, and reviews which provide different perspectives, earlier works or peripheral subjects in great detail[1-6]. 'The Silk Proteins' by Lucas et al. serves as a compendium of basic information on the chemistry and biology of silk proteins.

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