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Postembryonic Development

1. Introduction

During their postembryonic growth period insects pass through a series of stages (instars) until they become adult, the time interval (stadium) occupied by each instar being terminated by a molt. Apterygotes continue to grow and molt as adults, periods of growth alternating with periods of reproductive activity. In these insects structural differences between juvenile and adult instars are slight, and their method of development is thus described as ametabolous. Among the Pterygota, which with rare exceptions do not molt in the adult stage, two forms of development can be distinguished. In almost all exopterygotes the later juvenile instars broadly resemble the adult, except for their lack of wings and incompletely formed genitalia. Such insects, in which there is some degree of change in the molt from juvenile to adult, are said to undergo partial (incomplete) metamorphosis, and their development is described as hemimetabolous. Endopterygotes and a few exopterygotes have larvae whose form and habits, by and large, are very different from those of the adults. As a result, they undergo striking changes (complete metamorphosis), spread over two molts, in the formation of the adult (holometabolous development). The final juvenile instar has become specialized to facilitate these changes and is known as the pupa (see also Chapter 2, Section 3.3).

In insect evolution increasing functional separation has occurred between the larval phase, which is concerned with growth and accumulation of reserves, and the adult stage, whose functions are reproduction and dispersal. Associated with this trend is a tendency for an insect to spend a greater part of its life as a juvenile, which contrasts with the situation in many other animals. Thus, in apterygotes, the adult stage may be considerably longer than the juvenile stage. Furthermore, feeding (in the adult) serves to provide raw materials both for reproduction and for growth. In exopterygotes and primitive endopterygotes adults may live for a reasonable period, but this is not usually as long as the larval phase. Feeding in the adult stage is primarily associated with reproductive requirements, though in some insects it provides nutrients for an initial, short "somatic growth phase" in which the flight muscles, gut, and cuticle become fully developed. Many endopterygotes live for a relatively short time as adults and may feed little or not at all because sufficient reserves have been acquired during larval life to satisfy the needs of reproduction.

2. Growth

2.1. Physical Aspects

Growth in insects and other arthropods differs from that of mammals in various respects. In insects growth is almost entirely restricted to the larval instars, though in some species there is a short period of somatic growth in newly enclosed adults when additional cuticle may be deposited, and growth of flight muscles and the alimentary canal may occur. As a consequence, the length of the juvenile stage is considerably longer than that of the adult. An extreme example of this is seen in some mayfly species whose aquatic juvenile stage may require 2 or 3 years for completion, yet give rise to an adult that lives for only a few hours or days. Growth in many animals is discontinuous or cyclic; that is, periods of active growth are separated by periods when little or no growth occurs. Nowhere is discontinuous growth better seen than in arthropods, which must periodically molt their generally inextensible cuticle in order to significantly increase their size (volume). It should be appreciated, however, that, though increases in volume may be discontinuous, increases in weight are not (Figure 21.1). As an insect feeds during each stadium, reserves are deposited in the fat body, whose weight and volume increase. In a hard-bodied insect this increase in volume may be compensated for by a decrease in the volume occupied by the tracheal system or by extension of the abdomen as a result of the unfolding of intersegmental membranes. In many endopterygote larvae, of course, the entire body is largely covered with extensible cuticle, and body size increases almost continuously (but see below).

For many insects grown under standard conditions the amount of growth that occurs is predictable from one instar to the next; that is, it obeys certain "growth laws." For example, Dyar's law, based on measurements of the change in width of the head capsule which occurs at each molt, states that growth follows a geometric progression; that is, the proportionate increase in size for a given structure is constant from one instar to the next. Mathematically expressed, the law states $x/y = \text{constant}$ (value usually 1.2–1.4), where $x =$ size in a given instar and $y =$ size in previous instar (Figure 21.1). Thus, when the size of a structure is plotted logarithmically against instar number, a straight line is obtained, whose gradient is constant for a given species (Figure 21.2). In those insects where it applies Dyar's law can be used to determine how many instars there are in the life history. However, so many factors

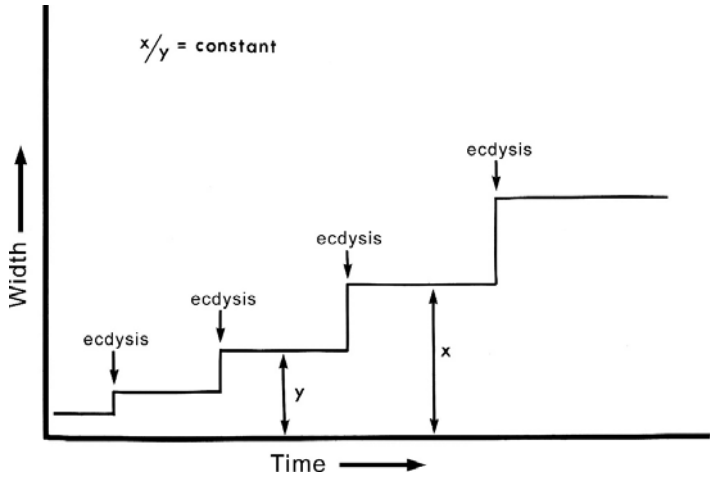

FIGURE 21.1. Change in head width with time to illustrate Dyar's law.