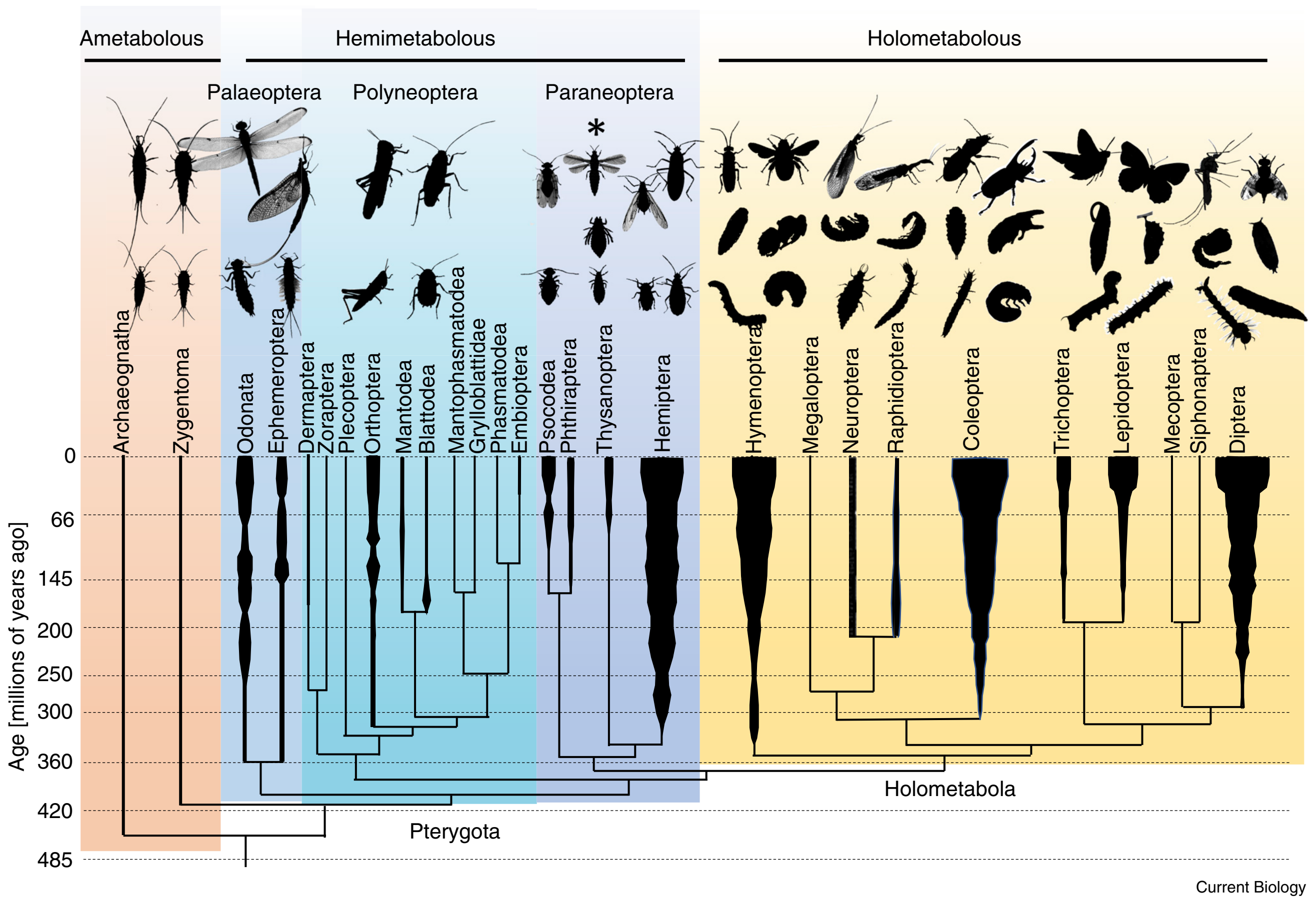

Figure 1. Phylogeny of insects showing the major types of development.
The figure shows how the three major types of insect development, ametabolous, hemimetabolous and holometabolous, map onto insect phylogeny, with examples of the immature and adult stages for each. The asterisk indicates neometabolous forms that have independently evolved a life history with a larva, pupa and adult. For the major orders the width of the boxes show the number of families through time. Phylogeny from [134,135] with family distributions adapted from [14] based on [136].

suppression techniques can be woven into a rich history of endocrine experimentation. Although these few systems do not begin to cover the amazing range of variation that one sees in the insects, it is heartening that highly derived life history strategies, such as female neoteny in Strepsiptera [4,5] and scale insects [6] or the complete metamorphosis that evolved in parallel in thrips [7], utilize the same molecular switches that regulate more traditional life history patterns. This review explores the developmental changes that accompanied the evolution of the insect larval and pupal stages. It then focuses on the two main hormonal systems that regulate insect molting and metamorphosis and considers how these systems evolved to support the increasing complexity of insect life histories. Finally, it examines our growing knowledge of the function of the stage specification genes that regulate the phenotype of each major life stage and how these genes and their control have changed with the increasing complexity of insect life histories.

Insect Life History Strategies

Because their rigid exoskeleton constrains growth and changes in morphology, an insect's life history is punctuated by molts, during which a new cuticle is formed and the old one shed, a process termed ecdysis. Consequently, the growth of the juvenile alternates between a period of feeding and growth (the intermolt) and a molt. The span from one ecdysis to the next is termed an instar. In most insects, there is a characteristic number of instars between hatching and metamorphosis, but the decision to begin metamorphosis typically depends on reaching a characteristic species-specific size [8]. Therefore, suboptimal nutrition or injuries or disease may result in the intercalation of additional molts until this size is achieved. Insects are extremely diverse in their feeding strategies, however, and in some species the larva can opt for an earlier instar to start metamorphosis if food conditions are poor (for example [9]).

By any criteria, insects are a spectacularly successful terrestrial group with diverse life history strategies and 28 extant orders (Figure 1). The true insects and other hexapods such as springtails (Collembola) and diplurans (Diplura) diverged from their aquatic crustacean ancestors and were part of the arthropod invasion of land that began over 450 million years ago. The life history of these earliest insects was similar to those of the jumping bristletails (Archaeognatha) and silverfish (Zygentoma) of today. These primitively wingless insects have an *ametabolous* lifestyle which shows direct development: the hatchling is a miniature