CHAPTER I

INTRODUCTION

AMONG the manifold operations of living creatures few have more strongly impressed the casual observer or more deeply interested the thoughtful student than the transformations of insects. The schoolboy watches the tiny green caterpillars hatched from eggs laid on a cabbage leaf by the common white butterfly, or maybe rears successfully a batch of silkworms through the changes and chances of their lives, while the naturalist questions yet again the 'how' and 'why' of these common though wondrous life-stories, as he seeks to trace their course more fully than his predecessors knew.

Everyone is familiar with the main facts of such a life-story as that of a moth or butterfly. The form of the adult insect (fig. 1 *a*) is dominated by the wings—two pairs of scaly wings, carried respectively on the middle and hindmost of the three segments that make up the *thorax* or central region of the insect's body. Each of these three segments carries a pair of legs. In front of the thorax is the head on which the pair of long jointed feelers and the pair

of large, sub-globular, compound eyes are the most prominent features. Below the head, however, may be seen, now coiled up like a watch-spring, now stretched out to draw the nectar from some scented blossom, the butterfly's sucking trunk or proboscis, situated between a pair of short hairy limbs or palps (fig. 2). These palps belong to the appendages of the hindmost segment of the head, appendages which in insects are modified to form a hind-lip or *labium*, bounding the mouth cavity below or behind. The proboscis is made up of the pair of jaw-appendages in front of the labium, the *maxillae*, as they are called. Behind the thorax is situated the *abdomen*, made up of nine or ten recognisable segments, none of which carry limbs comparable to the walking legs, or to the jaws which are the modified limbs of the head-segments. The whole cuticle or outer covering of the body, formed (as is usual in the group of animals to which insects belong) of a horny (chitinous) secretion of the skin, is firm and hard, and densely covered with hairy or scaly outgrowths. Along the sides of the insect are a series of paired openings or spiracles, leading to a set of air-tubes which ramify throughout the body and carry oxygen directly to the tissues.

Such a butterfly as we have briefly sketched lays an egg on the leaf of some suitable food-plant, and there is hatched from it the well-known crawling

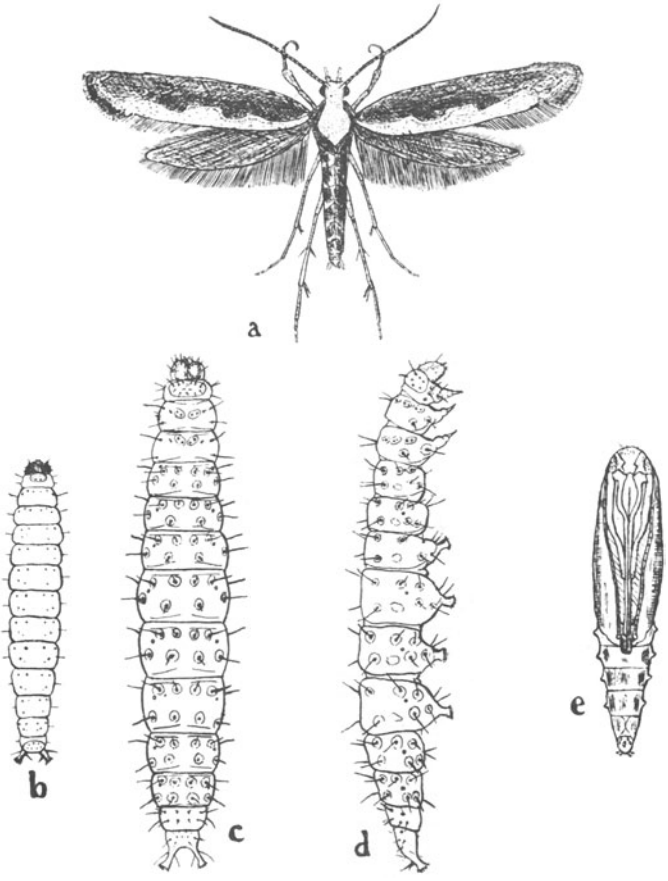

Fig. 1. *a*, Diamond-back Moth (*Plutella cruciferarum*); *b*, young caterpillar, dorsal view; *c*, full-grown caterpillar, dorsal view; *d*, side view; *e*, pupa, ventral view. Magnified 6 times. From *Journ. Dept. Agric. Ireland*, vol. 1.

larva[1] (fig. 1 *b, c, d*) called a caterpillar, offering in many superficial features a marked contrast to its parent. Except on the head, whose surface is hard and firm, the caterpillar's cuticle is as a rule thin and flexible, though it may carry a protective armature of closely set hairs, or strong sharp spines. The feelers (fig. 3 *At*) are very short and the eyes are small and simple. In connection with the mouth, there are present in front of the maxillae a pair of *mandibles* (fig. 3 *Mn*), strong jaws, adapted for biting solid food, which are absent from the adult butterfly, though well developed in cockroaches, dragon-flies, beetles, and many other insects. The three pairs of legs on the segments of the thorax are relatively short, and as many as five segments of the abdomen may carry short cylindrical limbs or pro-legs, which assist the clinging habits and worm-like locomotion of the caterpillar. No trace of wings is visible externally. The caterpillar, therefore, differs markedly from its parent in its outward structure, in its mode of progression, and in its manner of feeding; for while the butterfly sucks nectar or other liquid food, the caterpillar bites up and devours solid vegetable substances, such as the leaves of herbs or trees. It is well-known that between the close of its larval life and its attainment of perfection as a butterfly,

[1] The term *larva* is applied to any young animal which differs markedly from its parent.

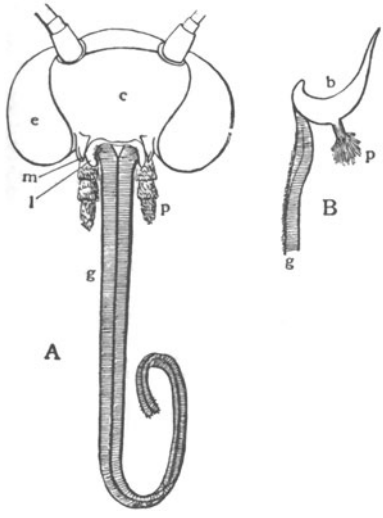

Fig. 2.

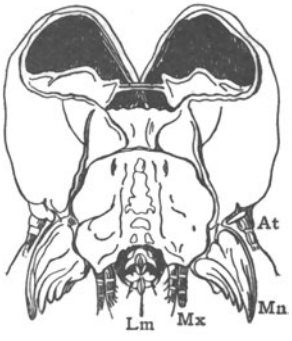

Fig. 3.

Fig. 2. A. Head of a typical Moth, showing proboscis formed by flexible maxillae (*g*) between the labial palps (*p*); *c*, face; *e*, eye; the structure *m* has been regarded as the vestige of a mandible. B. Basal part (*b*) of maxilla removed from head, with vestigial palp (*p*). Magnified.

Fig. 3. Head of Caterpillar of Goat-moth (*Cossus*) seen from behind. *At*, feeler; *Mn*, mandible; *Mx*, maxilla; *Lm*, labium, spinneret projecting beyond it. Magnified. After Lyonet from Miall and Denny's *Cockroach*.

the insect spends a period as a *pupa* (fig. 1 *e*) unable to move from place to place, and taking no food.

Such, in brief, is the course of the most familiar of insect life-stories. For the student of the animal world as a whole, this familiar transformation raises some startling problems, which have been suggestively treated by F. Brauer (1869), L. C. Miall (1895), J. Lubbock (1874), R. Heymons (1907), P. Deegener (1909) and other writers[1]. To appreciate these problems is the first step towards learning the true meaning of the transformation.

The butterfly's egg is absolutely and relatively of large size, and contains a considerable amount of yolk. As a rule we find that young animals hatched from such eggs resemble their parents rather closely and pass through no marked changes during their lives. A chicken, a crocodile, a dogfish, a cuttlefish, and a spider afford well-known examples of this rule. Land-animals, generally, produce young which are miniature copies of themselves, for example horses, dogs, and other mammals, snails and slugs, scorpions and earthworms. On the other hand, metamorphosis among animals is associated with eggs of small size, with aquatic habit, and with relatively low zoological rank. The young of a starfish, for example, has hardly a character in common with its parent, while a marine

[1] The dates in brackets after authors' names will facilitate reference to the Bibliography (pp. 124–8).

segmented worm and an oyster, unlike enough when adult, develop from closely similar larval forms. If we take a class of animals, the Crustacea, nearly allied to insects, we find that its more lowly members, such as 'water-fleas' and barnacles, pass through far more striking changes than its higher groups, such as lobsters and woodlice. But among the Insects, a class of predominantly terrestrial and aerial creatures producing large eggs, the highest groups undergo, as we shall see, the most profound changes. The life-story of the butterfly, then, well-known as it may be, furnishes a puzzling exception to some wide-reaching generalisations concerning animal development. And the student of science often finds that an exception to some rule is the key to a problem of the highest interest.

During many centuries naturalists have bent their energies to explain the difficulties presented by insect transformations. Aristotle, the first serious student of organised beings whose writings have been preserved for us, and William Harvey, the famous demonstrator of the mammalian blood circulation two thousand years later, agreed in regarding the pupa as a second egg. The egg laid by a butterfly had not, according to Harvey, enough store of food to provide for the building-up of a complex organism like the parent; only the imperfect larva could be produced from it. The larva was regarded as

feeding voraciously for the purpose of acquiring a large store of nutritive material, after which it was believed to revert to the state of a second but far larger egg, the pupa, from which the winged insect could take origin. Others again, following de Réaumur (1734), have speculated whether the development of pupa within larva, and of winged insect within pupa might not be explained as abnormal births. But a comparison of the transformation of butterflies with simpler insect life-stories will convince the enquirer that no such heroic theories as these are necessary. It will be realised that even the most profound transformation among insects can be explained as a special case of growth.

CHAPTER II

GROWTH AND CHANGE

THE caterpillar differs markedly from the butterfly. As we pursue our studies of insect growth and transformation we shall find that in some cases the difference between young and adult is much greater—as for example between the maggot and the house-fly, in others far less—as between the young and full-grown grasshopper or plant-bug. It is evidently wise to begin a general survey of the subject with some of

those simpler cases in which the differences between the young and adult insect are comparatively slight. We shall then be in a position to understand better the meaning of the more puzzling and complex cases in which the differences between the stages are profound.

In the first place it is necessary to realise that the changes which any insect passes through during its life-story are essentially accompaniments of its growth. The limits of this little book allow only slight reference to features of internal structure; we must be content, in the main, to deal with the outward form. But there is an important relation between this outward form and the underlying living tissues which must be clearly understood. Throughout the great race of animals—the Arthropoda—of which insects form a class, the body is covered outwardly by a *cuticle* or secretion of the underlying layer of living cells which form the outer skin or *epidermis*[1] (see fig. 10 *ep*, *cu*, p. 39). This cuticle has regions which are hard and firm, forming an *exoskeleton*, and, between these, areas which are relatively soft and flexible. The firm regions are commonly segmental in their arrangement, and the intervening flexible connections render possible accurate motions of the exoskeletal parts in relation

[1] The term 'hypodermis' frequently applied to this layer is misleading. The layer is the true outer skin—ectoderm or epidermis.

to each other, the motions being due to the contraction of muscles which are attached within the exoskeleton.

Now this jointed exoskeleton—an admirably formed suit of armour though it often is—has one drawback: it is not part of the insect's living tissues. It is a cuticle formed by the solidifying of a fluid secreted by the epidermal cells, therefore without life, without the power of growth, and with only a limited capacity for stretching. It follows, therefore, that at least during the period through which the insect continues to grow, the cuticle must be periodically shed. Thus in the life-story of an insect or other arthropod, such as a lobster, a spider, or a centipede, there must be a succession of cuticle-castings—'moults' or *ecdyses* as they are often called.

When such a moult is about to take place the cuticle separates from the underlying epidermis, and a fluid collects beneath. A delicate new cuticle (see fig. 10 *cu'*) is then formed in contact with the epidermis, and the old cuticle opens, usually with a slit lengthwise along the back, to allow the insect in its new coat to emerge. At first this new coat is thin and flabby, but after a period of exposure to the air it hardens and darkens, becoming a worthy and larger successor to that which has been cast. The cuticle moreover is by no means wholly external. The greater part of the digestive canal and the whole