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CHAPTER I

INTRODUCTION

FROM the earliest times the insect larva has been regarded as an embryo enjoying an independent life. For Aristotle taught that the embryonic life of insects continues until the formation of the perfect insect or imago: 'the larva while it is yet in growth', he writes, 'is a soft egg.' The insect egg, according to William Harvey (1651), contains so little yolk that the embryo is forced to leave it before development is complete: it requires a larval stage in which to store up food material, until it reverts once more to the egg form or pupa. Ramdohr (1811) still retains the same idea and calls the caterpillar a 'moving, growing and feeding egg'; and so, indeed, does Viallanes (1882), who writes of 'those sorts of eggs that are called nymphs or pupae'.

Lubbock (1883) likewise traces the origin of metamorphosis to the immaturity in the condition of the insect at the time of hatching. Such an insect as the cockroach, as it develops in the egg, goes through a protopod phase, a polypod phase and an oligopod phase. According to the conception outlined by Lubbock the different groups of insects hatch from the egg at one or other of these developmental stages.

This idea, which was characterized by Pérez (1902) as 'bizarre', was later elaborated by Berlese (1913) and has been given wide currency in the writings of Imms (1925, 1937). It is often referred to as the Berlese theory. According to this 'theory' the newly hatched young of such insects as Adephaga, Staphylinidae, Meloidae, Strepsiptera or *Mantispa*, which bear a general resemblance to the primitive *Campodea*, do not leave the egg until they have reached the oligopod phase. The caterpillars of Lepidoptera, Tenthredinidae or Mecoptera, with abdominal appendages, are regarded as having hatched in the polypod phase. The larvae of other Hymenoptera and Coleoptera, with no abdominal appendages, are pictured as being between the

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polypod and oligopod phases, and the larvae of Diptera as being oligopod but highly modified. All these forms, which are supposed to leave the egg at an early stage of morphological development, are commonly termed 'larvae'; whereas such forms as Orthoptera, Hemiptera, Odonata, etc., which are supposed to leave the egg at a relatively advanced stage, are commonly termed 'nymphs'.

POLYMORPHISM. This approach to the problem of metamorphosis, in which the larva is seen as some kind of embryo, may have a certain value for descriptive purposes; but it is very different from the conception of insect growth that comes from a study of developmental physiology. Growth in the insect is not so very different from that in other animals. There are changes in form as growth proceeds; and since the form of the insect body is defined by an external cuticle, which remains unchanged throughout each moulting stage, it follows that any alteration in form must occur suddenly as the cuticle is shed, or must at least take place in a series of steps each more or less abrupt. This has the effect of making metamorphosis appear more catastrophic than it really is (Lubbock, 1883). But even allowing for this the changes in form are spectacular enough.

Now difference in form or polymorphism is almost universal among animals. There are differences between young and mature, between male and female, between the forms appearing in the cold or wet season and those appearing in the hot season or the dry. There are differences in caste between workers, soldiers and reproductives in ants and termites, or differences in successive or alternate generations. Metamorphosis is merely one type of polymorphism.

The polymorphic organism generally contains within it the potentialities for all its diverse forms. Sometimes the form to be developed is determined by the genetic constitution; but not uncommonly the genetic constitution is overridden by the environmental conditions experienced during growth. The 'penetrance' of genes may be influenced by temperature, or by nutrition. The genetically determined sex of Hymenoptera or Homoptera may be reversed in the course of development as the result of parasitism by Strepsiptera or dryinids. In ants and termites the potentialities to form all the female castes exist in every female egg; which castes appear is determined by the needs of their societies, acting by way of stimuli that are very incompletely understood.

Lubbock drew a distinction between animals with different terminal or mature forms (polymorphism) and animals which pass through a succession of different forms in the course of their development (polyeidism). It is doubtful whether there is anything fundamental about this distinction. The essential feature of polymorphism is multiple potentiality: one form alone is realized; the others remain latent or suppressed. The characteristic of metamorphosis is that this suppression is only temporary; so that one form replaces another during the normal life of the individual.

EMBRYOLOGY AND METAMORPHOSIS. It is obvious, as Swammerdam (1758) rightly maintained, that the latent form must exist, in some state which we do not understand, within the undeveloped organism. This applies equally to the embryonic germ in the egg; and the egg of insects has proved particularly well suited for studying the progressive determination and differentiation of this latent organism. When the egg is laid the single nucleus or germinal vesicle lies at the centre of the yolk and the egg plasma radiates from it, enclosing in its meshes the reserve substances of the yolk, to condense around the surface of the egg as the cortical plasma. One limited region of the cortical plasma, sometimes (as in *Tenebrio* (Ewest, 1937)) distinguishable visually from the remainder, and lying in the postero-ventral region of the egg, is already destined to become the embryo.

At this stage the non-cellular germ of the organism is highly plastic; it is still capable of 'regulation'. If one part is removed it is made good and a complete organism develops from the remainder. If it is divided, two complete organisms are differentiated. Then the nucleus undergoes cleavage; the daughter nuclei as they divide repeatedly move outwards and eventually reach the cortical plasma. Those nuclei which fall within the germ band zone are destined to contribute to the embryo; those which arrive elsewhere form only the extra-embryonic blastoderm.

At some stage in this process the germ band loses its capacity for complete regulation. Each part becomes committed to form some part of the embryo. The egg becomes an invisible mosaic of determined zones. This change to the mosaic state is gradual, and in many eggs some capacity for regulation persists until a late stage; but the main change can be recognized as occurring in different eggs at quite different stages of cleavage or blastoderm formation. In the dragonfly *Platycnemis*, regulation is still possible in the late blastoderm stage (Seidel, 1936); in *Sialis* determination occurs between the fourth and fifth cleavages, at the moment when the blastema is formed by peripheral migration of the cytoplasm (Du Bois, 1938); in *Bruchus* the posterior cytoplasmic regions of the egg are determined before the entrance of the cleavage nuclei, the more anterior parts shortly after the cleavage cells arrive (Brauer and Taylor, 1936); whereas in *Musca* determination of the cortical plasma is complete at the time of laying before cleavage has even begun (Reith, 1925).

In *Drosophila*, as in *Musca*, the egg at the time of laying is a mosaic egg. Local injuries effected by burning with a pencil of ultra-violet light immediately after laying cause local defects in the resulting larva. But the adult characters are unaffected; in respect to imaginal characters the egg is still capable of 'regulation'. If the egg is similarly treated 7 hours after laying or later, localized defects appear in the adult—often without any visible effect during larval development (fig. 1) (Geigy, 1931). Similar results can be obtained by puncturing the egg at different levels with a needle (Howland and Child, 1935; Howland and Sonnenblick, 1936). Likewise in *Tineola*, by burning different points in the egg with ultra-violet irradiation at different times it is possible to obtain purely larval or purely imaginal defects (Lüscher, 1944). It is clear that even at this early stage of embryonic development certain parts of the germ have already become determined to form specialized parts of the adult insect.

ORIGIN AND EVOLUTION OF METAMORPHOSIS. These observations serve to demonstrate the independent existence within the embryo of two latent organisms, larval and adult. As development proceeds the larval organism becomes differentiated, hatches and grows, while the adult organism remains in its latent, mosaic, invisible condition. This state of affairs persists until the larva is full grown; it then disappears and the adult organism becomes visibly differentiated. It is this change that is called metamorphosis. It is often regarded as a renewal of embryonic development, in that the process of transition from a state of invisible determination to a state of visible differentiation is the same in both.

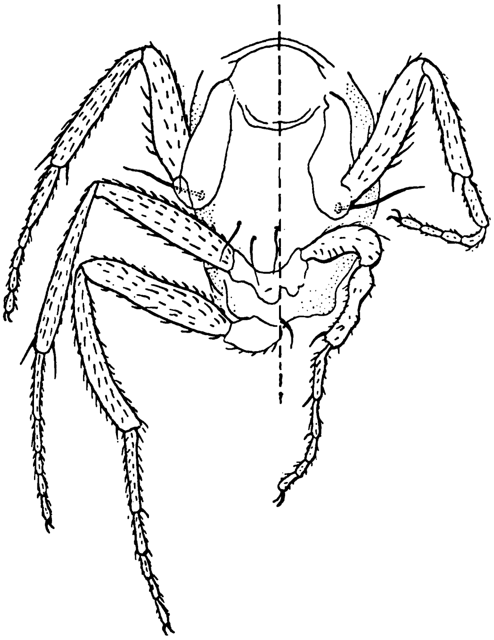

Fig. 1. *Drosophila* adult showing complete suppression of left hind-leg with deformation of first and second leg on the same side, following unilateral irradiation of the egg with ultra-violet light. Larval stages showed no visible defects. (Geigy, 1931.)

The important point at this stage of the argument is the independence of the alternative forms in which polymorphic organisms can exist. It is by virtue of this independence that these forms are capable of separate evolution. The same applies to the successive forms that exist in insects showing a metamorphosis. The larva is subject to the influence of its environment, and by the action of natural selection (or whatever other agencies control organic change) it may undergo an evolution of

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its characters which leaves the adult insect untouched. Larvae of the silkworm or of the gipsy moth *Lymantria* (Klatt, 1919) exist in many very different genetic racial forms which cannot be differentiated in the adult state. Indeed, certain species of Lepidoptera (such as *Acronycta psi* and *A. tridens*) distinguishable with great difficulty in the adult have very different larvae. On the other hand, highly polymorphic butterflies such as *Papilio polytes* show no corresponding differences in their caterpillars. A similar independence is seen in the pupa: the female of *P. dardanus* has no tails on the hind-wing, but pockets are provided for them in the pupal wing cases (Lamborn, 1914), and in the wingless mutant of the silkworm the wing cases of the pupa are formed as usual (Goldschmidt, 1927).

It follows, therefore, that as soon as there are differences in the mode of life of an adult insect and its larva the characters of the two forms will tend to diverge, and such divergence may reach the extreme that separates the maggot from the fly. Lubbock recognized that the form of the larva is affected by phylogenetic influences on the one hand and by adaptive influences on the other. Writing in 1883, at a time when the theory of recapitulation exerted a greater influence than it does to-day, he was inclined to give greater weight to the importance of phylogeny. At the present day we are inclined to reverse this emphasis: to regard the larva as a highly specialized form, closely adapted to the conditions of its life, whose resemblance to an embryo is superficial and adventitious (cf. Müller, 1869; Schindler, 1902; Snodgrass, 1953).

ORIGIN OF THE PUPA. The origin of metamorphosis is to be sought, therefore, in the divergent evolution of a polymorphic organism. The same considerations apply to the pupa in holometabolous insects. Perhaps the most obvious function of the pupa is that it bridges the morphological gap between the larva and the fully developed adult. But here again the best guide is to regard the pupa as the product of independent evolution in one form in a polymorphic organism to suit the ecological or anatomical needs of the insect in question.

Attempts have been made to find a single overriding final cause which has necessitated the development of the pupa. One of the most attractive is the view put forward by Poyarkoff (1914) and developed by Hinton (1948) that the skeletal muscles require a 'mould' in which the cuticular parts have approximately the same spatial relations as in the adult, and that a pupal mould becomes necessary when the anatomical differences are so great that the muscles required by the adult cannot be formed in the larva. But as Weber (1952) points out, the aleurodids are able to develop directly at a single moult from an extremely flattened scale-like larva to a fully winged and long-legged adult.

IMAGINAL DISCS. The classic discussions of insect metamorphosis have always centred around the more extreme examples, such as the Lepidoptera, Hymenoptera or Diptera. The anatomical study of these forms led to the discovery of the 'imaginal discs' (Lyonet, 1762), the significance of which was first appreciated by Weismann (1864), in his work on *Calliphora*, as nests of embryonic cells set aside for the formation of the adult. They represent the latent imaginal organism in visible form; and physiological discussion turned upon what factors inhibit the development of the imaginal discs in the young stages, or cause the larval tissues to disintegrate and activate the imaginal buds at metamorphosis.

It has been suggested, for example, (i) that the imaginal discs are held quiescent by the excretory products of the active larval tissues, and when these begin to degenerate the adult tissues can begin to grow (Anglas, 1901); (ii) that the larval tissues give out substances which keep the phagocytic blood cells at bay; when they age they become a prey to phagocytes and the imaginal discs develop in their place (Kowalevsky, 1887; v. Rees, 1888); (iii) that asphyxia in the larval tissues causes their degeneration (Bataillon, 1893); (iv) that the oxidase associated with melanin formation, which is at a maximum at the time of pupation, is in fact the *cause* of metamorphosis (Dewitz, 1916; cf. Agrell, 1951); (v) that the increasing size of the larval tissue cells set a physical limit to their ability to gain nourishment by diffusion (Murray and Tiegs, 1935; Tiegs, 1922); (vi) that secretions from the growing sex glands activate the imaginal discs (Pérez, 1902, 1910); (vii) that in the larva, the development of the imaginal discs is checked by secretions from the brain (Kopeč, 1924; but cf. Kopeč, 1927).

It will be observed that all these hypotheses relate to the inhibition or activation of imaginal discs. But many parts of the adult body, even in such insects as Lepidoptera or Hymenoptera which suffer a spectacular metamorphosis, are not formed from imaginal discs but are laid down by the same cells as have formed the larva. The general integument of the abdomen in adult Lepidoptera is very different from that of the caterpillar, but the same cells are concerned in its formation. In some insects the imaginal discs appear very early: in Diptera some are already evident in the late embryo (Enzmann and Haskins, 1938); in *Vanessa* the wing discs are present in the first larval stage, although those for the limbs do not appear until the end of the fourth stage (Bodenstein, 1935). But in every insect, if they are traced back far enough in development, the imaginal discs will be found to merge into the general epidermis of the larva or the embryo. There must, therefore, be a time, even in Lepidoptera or Diptera, when the same cells which are forming the visible larval structures carry latent within them the capacity to form imaginal structures.

We have already seen that this is so in the developing egg of *Drosophila* and *Tineola*. The purpose in elaborating the argument here is to emphasize that imaginal discs are not a necessary feature of metamorphosis, and that the essential problems of metamorphosis—the latency and subsequent realization of an imaginal organism—can be studied equally well in an insect in which imaginal discs do not occur.

METAMORPHOSIS IN *RHODNIUS*. It was on these grounds that the Hemipteron *Rhodnius prolixus* was chosen for the study of metamorphosis (Plate I *a–c*). *Rhodnius* has five larval stages throughout which the structural characters of the cuticle and the pigment pattern show little change. There is progressive growth and differentiation in the wing lobes, and in the later larval stages the rudiments of the genitalia begin to differentiate. But these changes are very slight in comparison with the metamorphosis which occurs when the 5th-stage larva moults to become adult.

Elaborate genital appendages are then developed: the thorax becomes elaborately shaped, with fully formed flight muscles; the wing lobes are transformed into large functional wings;

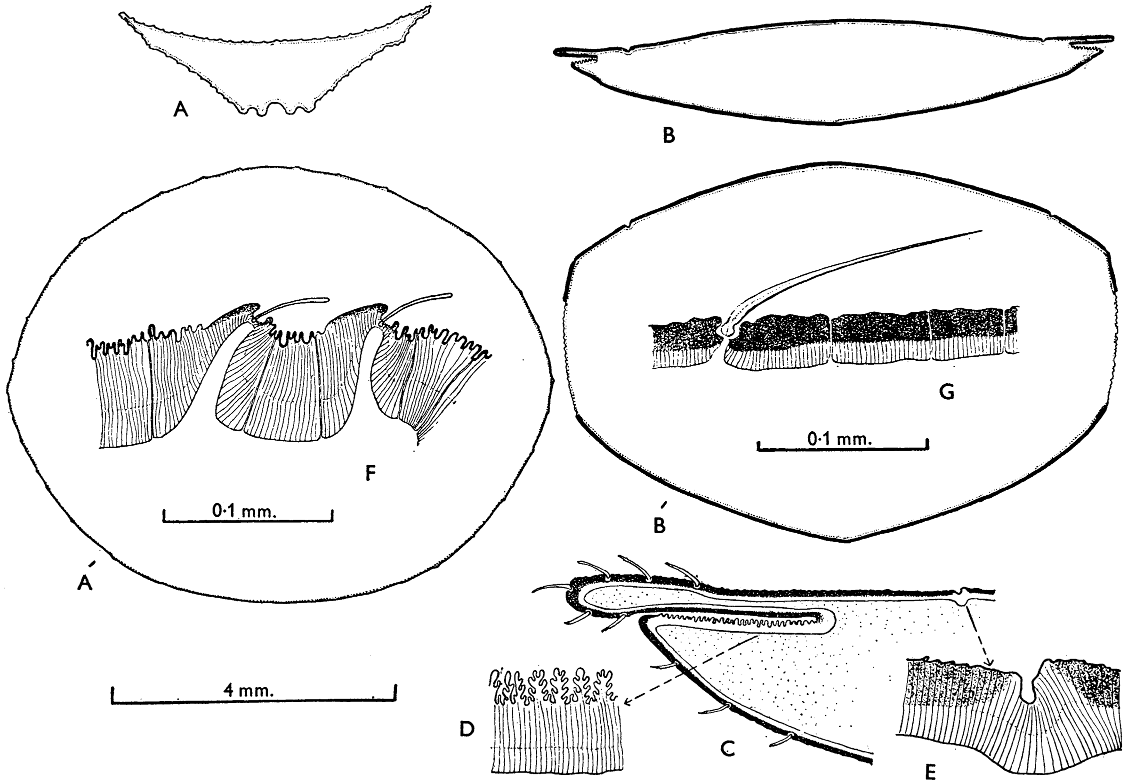

Fig. 2. A, transverse section of abdomen of unfed 5th-stage larva of *Rhodnius*. A′, ditto immediately after feeding. B, transverse section of abdomen of unfed adult. B′, ditto immediately after feeding. C, detail of lateral pleat in abdomen of unfed adult. D, detail of extensible lower wall of this pleat. E, detail of 'hinge-line' in tergites. F, longitudinal section of abdominal tergite in 5th-stage larva (cf. fig. 30A). G, longitudinal section of abdominal tergite of adult (cf. fig. 30H). (Wigglesworth, 1933.)

ocelli appear for the first time; a soft pad covered with tenent hairs to form a climbing or adhesive organ is differentiated at the end of the first and second tibiae; and the whole structure and pattern of the cuticle is changed. In the larva the cuticle of the abdomen is highly extensible, the epicuticle being thrown into deep stellate folds and beset with smooth rounded plaques each bearing a bristle. In the adult the surface of the abdominal cuticle is thrown into transverse folds; it is inextensible, without bristle-bearing plaques, distension of the abdomen being provided for, not by a general stretching of the cuticle but by the unfolding of a lateral pleat and the elasticity of a lateral strip of soft cuticle (fig. 2).

Throughout this book it is this example of metamorphosis which will occupy the centre of the stage. Full use will be made of all the evidence available from the study of other groups of insects; but it is obvious that the essential problem of metamorphosis is here displayed and if it can be elucidated in *Rhodnius* it will be equally clear in other forms. We shall not be concerned with problems of evolution, of adaptation, or of ecology. We shall treat only the physiological processes by which growth and change in form are regulated.

The physiological study of metamorphosis is concerned with the control of the emergence of the imaginal potentialities. We began this chapter with a reference to the embryological conception of metamorphosis which dates from Aristotle. The theory which interprets metamorphosis as an example of polymorphism is due to Swammerdam (1758). It implies the existence of a predetermined substrate upon which the physiological factors exert their controlling influence. The conception of development to which it leads is neither solely preformationist nor solely epigenetic. It is both.