RESEARCHES ON THE INSECT METAMORPHOSIS

PART I. ON THE POST-EMBRYONIC DEVELOPMENT OF A CHALCID WASP, NASONIA

PART II ON THE PHYSIOLOGY AND INTERPRETATION OF THE INSECT METAMORPHOSIS

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C O N T E N T S.

INTRODUCTION

The Insect Transformation presents one of the most interesting of the many phenomena of living things about us. To the popular imagination it is a manifestation of the supernatural. To the biologist it offers unrivalled material for the study of several fundamental tissue reactions: extensive tissue degenerations followed by correspondingly great tissue regenerations; delayed cell differentiation and cell regeneration and sometimes even, it seems, cellular dedifferentiation; while the cases of phagocytosis sometimes met with are extraordinary. Nevertheless its study has been very neglected.

Numbers of the great early anatomists - Malpighi, Swammerdam, Lyonet, Dürckheim - turned their attention to the structure of insects, and though they were able to show that the larvae of insects had already the same general anatomy as had the adult insects, yet the difficulties of the dissection of the soft semifluid contents of the pupal shell proved so great, that the process of transformation was not elucidated.

Réaumur, it is true, had been able to show that the limbs of the adult insect were to be found invaginated beneath the surface of the body of the nymph. Newport (1832) had observed the concentration of the ganglia of the ventral nerve cord as it changed from the larval to the imaginal condition, but beyond these facts nothing was known; and Oken, who wrote his voluminous "Allgemeine Naturgeschichte" at about this time (1836), summarised his knowledge of the process thus:- (Vol.5, p.714) "At the last moult the insects become covered by a horny shell, which is devoid of feet and oral appendages. Consequently in this stage they lie quiet for several weeks, often throughout the whole winter, without feeding or moving and in this condition are spoken of as Pupae or Nymphs.

Under this shell is gradually formed the perfect insect, the fly with its three body parts, with its new feeding organs, feet and wings; finally the skin splits dorsally, the insect creeps out, waits a few minutes till it has hardened, and then crawls or flies away, to seek other food or to reproduce. This gradual step-like development is spoken of as a Transformation or Metamorphosis".

It was not till the publication in 1864 of Weismann's great memoir on the metamorphosis of the blow-fly that any light was thrown on the process. Weismann, without any modern technique available to him, and using only the old method of hand dissections studied the process with remarkable accuracy. His observations were made more on broad general anatomical lines. He was able to show that the larval tissues underwent a process of disintegration -"histolysis" he called it - into rounded bodies, which he called Körnchenkugeln, and that the imago in turn was formed from small areas of cells, which Swammerdam had already discovered ~~discussed~~, though he had not recognised their significance; to these he gave the name "Imaginal Discs". He was able to demonstrate the sexual organs in a young condition in the larva, and to show that the insect metamorphosis was entirely different from the alternation of generations that occurred in some groups of animals and plants. He demonstrated the occurrence of metamorphosis in most of the organs of the body, including the heart, and nervous system, which other investigators with more elaborate technique at their disposal have since questioned; and though his observations were necessarily incomplete and did not extend largely to cell changes, yet his conclusions were, in the main, correct.

Since Weismann's memoir the blow-fly (Calliphora) has been used by a number of investigators for the study of metamorphosis, so that

our knowledge of the process in this insect, though still very incomplete, is much fuller than that of any other. In 1876 the Russian Ganin wrote upon it, and described the imaginal "nests" within the intestine. In 1884, Van Rees, and in the following year, quite independently Kowalevsky, guided by Metchnikoff's recent discovery of the phagocytic action of leucocytes, showed that the larval tissues were destroyed by the interference of these colourless corpuscles of the blood. A special interpretation was therefore placed on Weismann's histolysis, and the "Körnchenkugeln" proved to be nothing but gorged phagocytes, a fact the truth of which Metchnikoff had himself already perceived from the drawings given by Ganin.

Since that time a number of other observers have added details to the knowledge accumulated by the earlier workers:- Van Rees studied it in 1888; Lowne published a few obervations (mostly incorrect) in 1890 - 1895; Vaney wrote about it in 1902; while Pérez published his very detailed work in 1910.

In 1899, and later in 1901, Berlese published his observations, and seriously questioned the important rôle which the leucocytes played in the removal of the larval tissues. From the earlier writings it seems to follow that the leucocytes attack the living tissues, so that metamorphosis is, in part, brought about by more than usually highly endowed leucocytes. Berlese denied this conception entirely. As he appears to have been misunderstood by others, it is best to quote his own words (1901). "Phagocytosis never occurs, and amoebocytes only become active when the muscle has disintegrated through internal causes". By phagocytosis he evidently means the phagocytosis of <u>living</u> tissues; and his "amoebocytes" appear to be a congregation of various kinds of embryonic cells and leucocytes, though he does not specially mention

these. Pérez (1910), on the other hand, has taken precisely the opposite view, and regards the leucocytes as playing the main part in the destruction of tissues. "I think I have proved satisfactorily that the disintegration of the muscle is due to phagocytes and that there is no spontaneous fragmentation of this organ into sacrolytes as Berlese thought". I may say at once, that the study of the metamorphosis of Nasonia has led me to conclude that while neither statement is quite correct neither is wholly wrong; - phagocytes play a large part in the removal of larval tissues, but such tissues are always dead.

Besides the observations of these workers, others have been made on portions of the metamorphosis of other insects, but nothing so extensive as those made on the blow-fly exists. In 1875 - 1878 Künckel d'Herculais published his studies on the structure and transformation of the syrphid fly Volucella; Degener in more recent years has studied the transformation of the intestine in a number of insects; and Verson (1898) examined it in the silkworm. Pérez (1902) examined portions of the metamorphosis of the ant Formica rufa; Bauer studied the transformation of the brain in several insects; and in 1912 Günther investigated the development of the eye in Dytiscus. In 1910 Poyarkoff published his very interesting observations on the metamorphosis of a beetle Galeruca: he showed that, while some organs underwent the usual type of phagocytic hystolysis others (the integument and part of the intestine) passed through a remarkable process of cellular rejuvenation.

It may be said then, that while we possess a considerable knowledge of the main features of insect metamorphosis, on some of the fundamental facts much difference of opinion prevails. Why do the larval tissues disappear? Do the phagocytes kill them, or do they merely remove them after they have died? If the latter, then how is their death

brought about? If in one insect phagocytic histolysis occurs, and in another merely cellular rejuvenation, how are we to correlate the processes? It is these questions that I shall attempt to answer in the present paper. The histological changes undergone by some of the larva organs moreover have never been examined - heart, peripheral nerves, ventral nerve cord, and others, while the greatest differences of opinion prevail about the details of other organs such as the muscles and intestine.

An equally interesting question is the relation in which the insects which show a metamorphosis stand to those in which it is absent; this question has been discussed by Lubbock (1874), and more recently by Deegener (1909). Lubbock's conclusion, that the metamorphosis was made necessary because the larvae had different feeding habits and consequently different mouth-parts from those of the adult insects, is not very satisfactory. While it is true that the transition from one to the other would have to be slow and would have to take place during a resting stage, it fails to account for the metamorphosis of structures of almost negligible importance, such, for example, as the fine somatopleural members beneath the integument. It fails also to explain the metamorphosis of the feeding organs in insects in which the larvae and adults have the same feeding habits, such, for example, as many of the carnivorous beetles. Moveover, the real thing to show is why the larval form should ever have been evolved, necessitating the parallel evolution of a metamorphosis, when some insects, very successful in the struggle for existence, have got on so well without it. The conclusion of Deegener, that the larval form is a stage gradually inserted between the early embryo state and the adult, is undoubtedly quite correct and seems to be usually accepted to-day. Nevertheless he throws no light on the reason

why such a form should ever have been evolved, nor does he explain why it later transforms itself into the mature insect.

It was to answer these several questions that the present work was undertaken. The insect which I have employed is a small chalcid wasp Nasonia brevicornis, very common in Australia and America as a parasite on exposed pupae of muscid flies. According to Mr.A.A.Girault it is identical with Nasonia abnormis Boheman, from Europe, and is evidently of world-wide distribution. As the work proceeded I found myself at a disadvantage in that very little was known about the internal anatomy of chalcid wasps, while the study of the anatomy of the larvae had also been greatly neglected, and more than one very serious misinterpretation had been accepted as fact. I have therefore resolved to extend the scope of the paper. In the first portion the various organs of the larva and adult are described and a fairly detailed account of them is given as they transform from the larval to the adult conditions. In the second part I shall attempt to explain the physiological basis of the metamorphosis, and to discuss the factors which have underlain the evolution of the process.