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The Question of the Gradient-factor and its Function in Insect Metamorphosis

Observations to H. E. HINTON's paper:
The initiation, maintenance, and rupture of diapause: A new theory
(The Entomologist, 86, 279—291, 1953)

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In the mentioned paper, under the heading "Novák's theory of epigenesis" (pp. 287—289)[1]) some of the theses of the so called gradient-factor theory of insect metamorphosis (NOVÁK, 1951a, b, 1954, 1955) are discussed in detail. Having agreed with some of its suppositions, the author comes to the conclusion, that ". . . . it is shown that no intracellular factor with the attributes of Novák's gradient-factor exists" and he gives the following objections against its existence:

(1) "The secretion of the corpora allata does not merely permit growth. It positively influences growth in the direction of the larva . . . This is most strikingly shown by the fact, that the hormone will cause ontogenetic regressions in the characteristics of the tissues."

(2) "If a gradient-factor, such as that postulated by Novák, exists, it cannot be identical with the juvenile hormone, as he claims. The gradient-factor must promote growth towards the adult form, as witness its effect in embryogenesis."

3) "If an intracellular gradient-factor is indeed present in the embryonic cells, it resembles the prothoracic gland hormone and not the juvenile hormone . . . . , because it is not, like the prothoracic gland hormone, inhibited by the diapause hormone, where as the juvenile hormone is supposed to be".

These objections seem however to be due to a certain degree to a misunderstanding and they cannot be agreed out of the following reasons.

[1]) The characterising of the gradient-factor theory by the term „theory of epigenesis" does not seem very felicitous, so as it could call up a false impression, that it puts up the one of the two contradictions epigenesis and preformation to the detriment of the other. In the reality the theory does not interfere with the fact that the metazoan organism develops successively from the fertilized egg-cell, by the chemical composition of which is predestinated its morphogenesis under normal conditions, irrespective of the phylogenetical changes.

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Ad (1) a): According to the gradient-factor theory the effect of the juvenile hormone on both the larval development and the inhibition of metamorphosis depends merely in its general metabolism and growth favouring character. This conclusion is based in the analysis of its effect on the shape of the metathetelic forms, transitory between the last instar nymph and the adult, in the Lygaeid bug *Oncopeltus fasciatus Dal.*, produced by the implantations of the active corpora allata in different periods of the last instar (cf. Novák, 1951 b). This analysis has shown that in the presence of the juvenile hormone all parts of the body grow with approximatively equal rate, so that no change in form occurs. In absence of the juvenile hormone only certain parts of the body are able to grow whereas the other remain unchanged. The result of such a disproportionate growth is the change of form in the direction of imago, it means the metamorphosis. The growth of the larval parts of the body may be restored by the implantation of active corpora allata (source of the juvenile hormone) in any time of metamorphosis. This is in consent with the findings on the juvenile hormone effects in all other groups of metabolic insects. In Holometabola the change of form is increased by the subsequent, more or less complete, histolysis of the non growing larval parts. It is thus evident that what does itself manifest like the "growth in the direction of the larva" depends in the activation of growth of those parts of the body which miss the ability to grow by themselves.

b) It has been found that the secretion of the corpora allata does not influence exclusively the growth of the larval parts of the body, but it likewise conditions the growth of such pronouncedly imaginal structures like the follicular cells in the ovarioles of the adult female in many of the studied species (cf. Wigglesworth, 1936; Pfeiffer-Weed, 1945; Thomsen, 1942 etc.) and it is necessary for the normal development and function of both male and female sexual accessory glands. There is nothing to entitle the supposition that an other hormonal factor would be produced by the corpora allata beside of the juvenile hormone. This fact is in clear contradiction with some pretended specific "larvotropic" effect of the juvenile hormone but it is completely understood by the gradient-factor theory.

c) It may be shown that the juvenile hormone, by inducing the harmonic growth in place of the disproportionate one, actually reduces the growth of the imaginal parts of the body. But this is likewise in no contradiction with its generally metabolism and growth favouring character. In the presence of all necessary growth-activators (biocatalysators), the further factor limiting growth is the availlable food-stuff reserve. And it is clear, that, when imaginal parts of the body (it means those supposed to contain the gradient-factor) alone are able to grow, they dispose of the total food-stuff reserve of the body, whereas under the influence of the juvenile hormone, their share is reduced by the quantity consumed by the activated larval parts.

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d) In a seeming contradiction with the way of explanation following from the gradient-factor theory seem to be the results of the mentioned experiments by WIGGLESWORTH (1940) and PIEPHO (1950 etc.). The authors have succeeded in causing the adult insect to moult and they have found, that when in such a case the juvenile hormone in sufficient concentration was present, the moulted insect has shown a certain degree of reversal towards the larval form. Yet, in all of these experiments only the epidermal cells, their product — the cuticle and (or) their patterns were affected (cf. WIGGLESWORTH, 1940, p. 216: "This change did not affect ellaborate structures, such as genitalia . . . . "). And it has been shown by WIGGLESWORTH, that at least part of the epidermal cells, which are fully developed and functioning in the larval stage, survive through the metamorphosis until the adult stage having changed in their structure and the charcter of the cuticle deposited. They thus differ in their response to the juvenile hormone from both the typical larval cells which fade away during the metamorphosis and from the typical imaginal cells which develop at first during the metamorphosis. Each epidermal cell may be told to behave in this respect as the body as a whole. It is therefore not surprising when they respond in the mentioned experiments to the presence of the juvenile hormone, by the described changes in their appearence and secretory activity, even in the adult stage. Though the number of comparative experiments from different groups of insects is not yet sufficient to allow defenitive conclusions, it seems probable, that what is called larval type of epidermis (or cuticle) would be a specific response of the epidermal cells to the action of the juvenile hormone which would depend in a more uniform and abundant metabolism and secretory activity. In any way it is in no contradiction with the general growth and metabolism favouring effect of the juvenile hormone and its way of influencing morphogenesis as supposed by the gradient-factor theory.

Ad (2): According to the theory discussed, the juvenile hormone is identical with the hypothetical gradient-factor in its physiological function, it means, they both are general metabolism and growth favouring factors (biocatalysators). There is not sufficient basis to judge the differences in their chemical composition so far, but there is no reason to suppose any other except that conditioning the solubility of the first of them in the haemolymph. The difference in their morphogenetical effects can be explained completely by the difference in their disribution in the body.

The gradient-factor, being a desmo-ferment (desmo-hormone), is bound to the specific areas of the body — the gradients of the disproportionate (allometric) growth — from which it may perhaps spread during the periods of their most intensive growth into the direct neighbourhood. It means, when gradient-factor alone is acting, only those parts of the body containing it are able to grow. The growth is therefore in this case disproportionate, resulting in the metamorphosis and formation of the adult form.

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The juvenile hormone on the other hand, being a typical blood spread glandular hormone, comes into contact with all parts of the body (making of course itself manifest by the activation of growth only in those parts which are not able to grow by themselves, it means in those lacking the gradient-factor). Its effect results thus in the harmonic growth without the change of form which is the characteristic of the larval development.

Ad (3): The fact that he growth of both larval and imaginal parts of the body is inhibited during the diapause does not seem to favour the HINTON's conclusion, that there would be any difference between the juvenile hormone and the gradient-factor in their attitude towards the "diapause hormone" as supposed by HINTON. But before the HINTON's hypothesis, of the pupal diapause being caused by the effect of some specific "diapause hormone", would be shown experimentally, it is difficult to do not prefer the much more simple explanation of its cause, resulting from the experiments of WIGGLESWORTH (1936 etc.) showing, that the decapitation of *Rhodnius* in any time of its postembryonal development results in a stage of diapause which may be broken by implantation of the active neurosecretoric cells of protocerebrum, from the well known papers of WILLIAMS (1947, 1948 etc.) and from the investigation of BRYN M. JONES (1953) who has shown that the end of embryonal diapause in the embryo of *Locusta pardalina* coincids with the beginning of the secretory activity in the neurosecretoric brain cells. According to these experiments at least most of the cases of the insect diapause may be explained as a direct result of a temporary inhibition of the production of the so called activating hormone (WIGGLESWORTH 1952; NOVÁK, 1955 = moulting hormone KOPEČ 1922; WIGGLESWORTH 1934, 1940 etc.). Even the experiments of FUKUDA (1953), showing a humoral influence of the pupal suboesophageal ganglion in the female silkworm on the determination of the embryonal diapause in the offspring, do not seem to be a sufficient basis to suppose any other effect than a temporary suppression of the production of the activating hormone. And there is no contradiction between any of these experimental facts and the supposition of the gradient-factor.

It may thus be concluded, that even if the supposition of the gradient-factor remains to be so far no more than a rather probable working hypothesis enabling a simple and unic explanation of the facts on the insect metamorphosis, both histological and experimental so far known, it cannot be regarded as weakened by the discussed objections.

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