Some Hypotheses Concerning the Reactions of the Wing-Pattern of Ephestia kühniella Z. (Lep. Pyral.) to Temperature Treatment.

By

Henning Lemche.

(From the Zoological Laboratory of the Royal Danish Veterinary and Agricultural College. Copenhagen).

According to Kühn & Henke (1929) the pattern on the fore-wing of the pyralid moth *Ephestia kühniella* consists of four different "systems", each of which is regarded to vary independently, viz. the symmetry-bands, the shadow, the discoid spots, and the marginal spots. However, these authors disregard the fact that in many other Lepidoptera a distinct longitudinal design is found which interferes with the transverse ones, and in later papers by Kühn and his collaborators we find the same tendency, viz. to treat only the transverse designs.

In an earlier paper (Lemche 1944) the venous spots in the shadow of *Ephestia kühniella* have been shown to vary genetically, independently of the intermediate ground, and in a recent paper (Lemche 1945) I have attempted to show that a distinction between the longitudinal design and the transverse ones is necessary if we are to make a detailed morphological analysis of the pattern. However, it still remains to be demonstrated that the same view may be of use in morphogenetical investigations on the variation of the pattern in Lepidoptera, especially such as they have been carried out in temperature-experiments by the German school of scientists assembling around Kühn.

These authors (Feldotto 1933, Kühn & Henke 1936, Wulkopf 1936, Stubbe 1938) found that the different pattern-systems vary independently of each other when the pupae are treated with extreme temperatures in a certain (early) stage of the pupal life — as was found by Kühn (1926) in the case of *Argynnis paphia*. However, the curves illustrating this variability have a very irregular course which has not hitherto been explained.

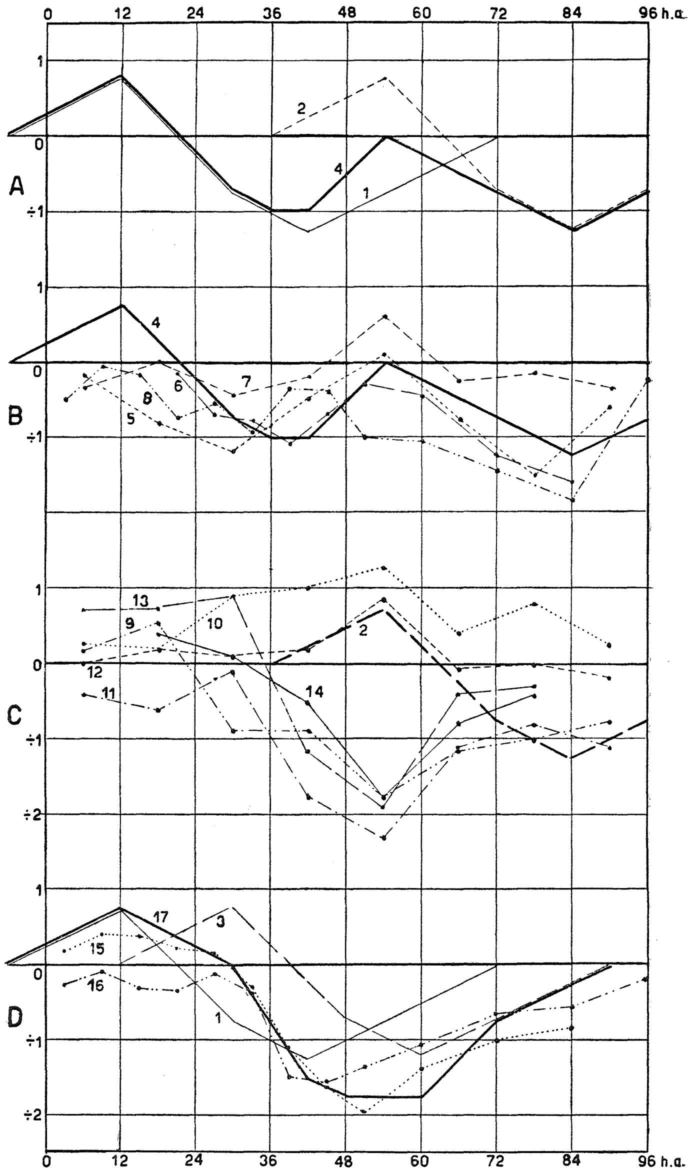
Now, on arriving at the result that the so-called systems are partly composed of two different designs, a transverse and a longitudinal one, it will be natural to transfer this view to the analysis of the temperature-variability also. However, since my stocks of genetically analyzed *Ephestia kühniella* have been given up several years ago, I have had no possibility of making new experiments for this purpose, and consequently I have to confine myself to a treatment of the records given by the authors cited above. I am well aware of the uncertainty necessarily associated with such a procedure, but the results obtained appear so simple that I am convinced of their correctness, at least as to their main points.

The papers of Feldotto (1933), Wulkopf (1936) and Stubbe (1938) agree in mentioning two successive minima in the variation of the symmetry-bands. The presence of two such minima may possibly be explained by supposing one of them to be due to the variation of the longitudinal design and the other to that of the transverse bands. Moreover, the shape of the curve shows the variability successively to strengthen and to weaken the darkening of the bands, whereas they retain their normal appearance when the impulse has been given too late.

If so, it may be possible to subtract from the total curve the part of it caused by the influence of the longitudinal design so that a relatively simple curve will result. Or, it may be possible to find two simple curves, each representing one of the designs involved, and to add them in such a way that the above mentioned, complicated curve results. The latter procedure being by far the simpler, I chose it for my attempt. By way of experiments I soon succeeded in finding a curve (the "basic curve") of a simple shape and resulting in the curve searched for when added to one of the same shape but with a different starting point (diagram A, curves 1 and 2, which by addition give curve 4). The agreement between the constructed curve and those actually found for the variation of the symmetry-bands is seen in diagram B.

Now, it may always be possible to construct a curve by adding two other curves of one shape or other, and hence it is necessary to check the result in some way. I wish, therefore, to point out at once that I have not altered the shape of these curves later on in order to obtain a better agreement with the variability of other systems than that used as a point of departure for the investigation. Hence the striking agreement between the suppositions, and — on the other hand — the results found empirically by different authors must be ascribed to other causes than a personal inclination to alter the theory to fit in with the facts.

In the case of the symmetry-system, the first of my partial curves (curve 1) starts at the normal value about 6 hours before the pupation; it has a maximum at a pupal age of about 12 hours (here designated as 12 h. a.), falling to the normal value at 20 h. a. and showing a minimum at 42 h. a. Finally, at 72 h. a. it reaches the normal value, i. e. from that time it shows no reaction to temperature shocks. The second curve must start at about 36 h. a. if addition to the first one shall result in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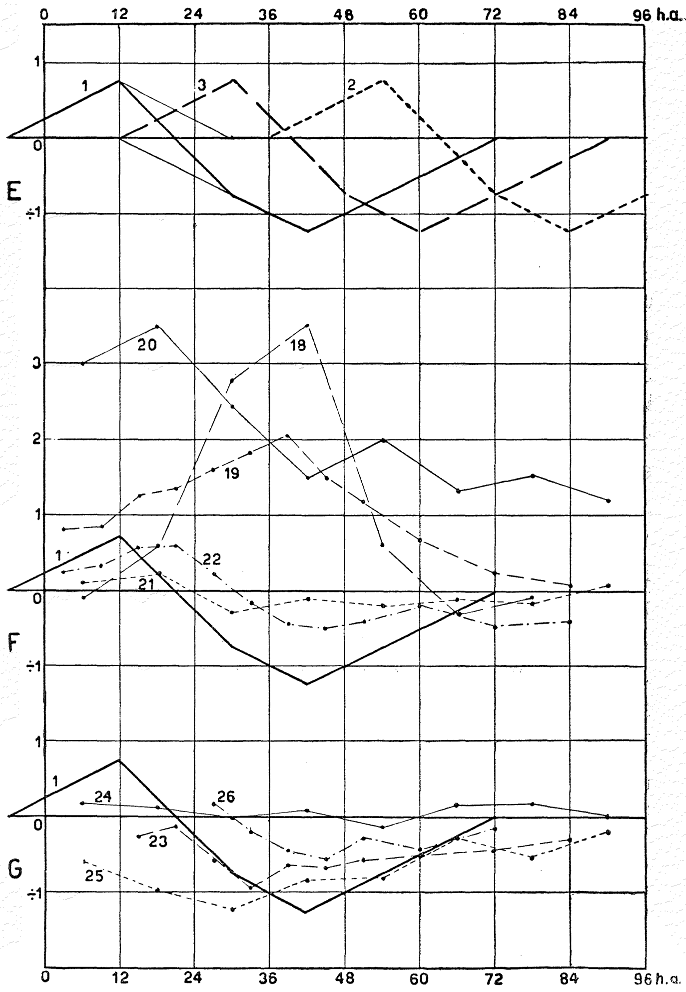

Diagrams A—G. Curves showing the reaction of the different parts of the pattern on the fore-wing of *Ephestia kühniella* when exposed to extreme temperatures during part of the pupal period. Abscissa: pupal age in hours (h. a.) when treated. Ordinate: Deviation from the normal appearance when emerging.

A. The construction of the curve of intensity of the symmetry-bands by means of the "basic curve". 1. Supposed reaction of the longitudinal design alone. 2. The same of the symmetry-bands proper. 4. The curve resulting from addition of 1 and 2.

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a curve which is in accordance with the empirical ones. By altering at the same time the starting points of the curves and their steepness, it will be possible to some extent to obtain similar results to that reached with the curves used here, but the differences appear to be only small and of no importance to the problems discussed here. The actual interrelation between the different designs may probably turn out to be far more complex than illustrated in these simple curves, which were prepared merely to show the principal features of the sensibility of the pattern.

An illustration of the reaction of the longitudinal design (curve 1) by a curve of exactly the same shape as those of the symmetry-bands (2) and the shadow-band (D, curve 3) must, of course, be just as arbitrary. However, in order to avoid the danger of losing myself in too intricate (and correspondingly indemonstrable) speculations I take it for granted that they are identical in all details except their starting points.

Although the curve of the symmetry-bands is shown to be divisible into two simpler curves, nothing can be

B. The intensity of the symmetry-bands after treatment: 5. by strong heat (Feldotto); 6. the same (Wulkopf); 7. the same (Stubbe); 8. by frost (Wulkopf).

C. The breadth of the central field when exposed to: 9. strong resp. 10. moderate heat (Stubbe, strain Kl. V); 11. resp. 12. the same (Stubbe, strain T. 19); 13. and 14. strong heat (Kühn & Henke, strains XIX and XI).

D. The intensity of the shadow after treatment by: 15. strong heat (Wulkopf), 16. frost (Wulkopf). 3. Supposed reaction of the shadow-band proper. 17. Total hypothetical variation of the shadow as resulting from addition of the curves 1 and 3.

E. The curves showing the hypothetical variation of the three designs involved, and the construction of the "basic curve".

F. The intensity of the marginal spots after treatment by: 18. strong heat (Feldotto); 19. the same (Wulkopf); 20. the same (Stubbe); 21. moderate heat (Stubbe); 22. frost (Wulkopf).

G. The intensity of the discoid spots after treatment by: 23. strong heat (Wulkopf); 24. the same (Stubbe); 25. moderate heat (Stubbe); 26. frost (Wulkopf).

deduced from this simple fact as to the possible interaction between longitudinal and transverse designs. But a close study of the illustrations given by the authors cited above showed that the first of the two curves represents the sensibility of the longitudinal design. If so, the second curve will show the alterations of the corresponding transverse design, and thus we are able to deduce something from the curves as to the appearance of the wings when treated at different stages. A treatment during the first part of the pupal life (about 0—24 h. a.) ought to strengthen the spots on the veins, whereas the band-ground between may behave as in the untreated animals. Unfortunately, no figures have been published of wings treated before attaining an age of 18 h. a., but several wings at the age of 18—24 h. a. show the variation expected (Kühn 1932 Abb. 3 b shows distinct black stripes along several veins, especially in the hind part of the wing, and a strong development of the venous spots, especially in DII (the outermost one of the symmetry-bands). Kühn & Henke 1936 Abb. 87 b is of a similar appearance, having a darker shadow but less distinct venous blackenings. Feldotto 1933 Abb. 26 b likewise shows distinct venous spots, especially in DII).

In the period 24—60 h. a. the spots, according to my hypothesis, will be indistinct and the ground dominate, but in the last part of that period small individual variations in the physiological age will suffice to alter the picture very considerably, and consequently we have better begin our study by confining ourselves to wings treated between 24 and 54 h. a. Feldotto 1933 Abb. 2 b, and Kühn 1932 Abb. 3 c (24—30 h. a.), as also Feldotto 1933 Abb. 2 c, 2 d and 7 b (30—36 h. a), and Kühn & Henke 1936 Abb. 87 c (24—36 h. a.) all agree in showing a very indistinct pattern except the marginal and the discoid spots. According to my hypothesis, this appearance is due to a decline in the intensity of the longitudinal design, whereas that of the transverse bands is unaltered.

At about 36 h. a. the strengthening of the colour of the ground of the symmetry-bands sets in, whereas the longitudinal design is still very indistinct. Consequently, we might expect a return to the normal, or nearly normal, blackening of the pattern, but with very indistinct spots on the veins. Kühn & Henke 1936 Abb. 87 d illustrates the appearance of such a wing — the narrowing of the central field is a special feature, which will be treated below. Gradually the longitudinal design reappears, and the increase in the strength of the pattern continues in the time from 48—54 h. a. (Feldotto 1933 Abb. 7 f and g, the latter of which is difficult to explain, but it appears to differ very much from the conditions generally found). The illustrations of the same author, Abb. 7 c, 7 d, 7 e and 13 b, and similarly Kühn 1932 Abb. 3 d, and Kühn & Engelhardt 1933 Abb. 5 c, show a very variable appearance of wings treated at 54—60 h. a., and so does the wing figured by Kühn & Henke 1936 Abb. 87 e (48—60 h. a.). At that time, the overnormal effect of the symmetry-bands diminishes and the longitudinal design reappears more and more, so that the inevitable difference of a few hours in the real physiological age of the different wings gives rise to the highly different results of the treatment. The wings shown by Feldotto 1933 Abb. 13 c (60—66 h. a.) and Kühn & Henke 1936 Abb. 87 f (60—72 h. a.) may be referred to the same transitional period. Finally, from about 72 h. a. to the period in which the loss of scales makes observation of the pattern impossible, the transverse symmetry-bands are very indistinct in spite of the normal impulses of the longitudinal design. This feature is illustrated by the wing reproduced by Feldotto 1933 Abb. 7 h (78—84 h. a.), which lacks almost every trace of pattern except the discoid spots (the shadow is very faintly developed in that stock). The wing figured by Kühn 1932 Abb. 3 e shows a later stage where the pattern reappears in a way so as to develop the spots before the ground.

The purpose of the survey given above of all the existing illustrations of *Ephestia*-wings treated in the first part of their pupal life (up to 96 h. a.) is to show that the published data are in full agreement with the hypothesis of two distinct but overlapping sensible periods, the first of which represents that of the longitudinal design, the second that of the symmetry-bands proper.

It may be worth mentioning that there is the best possible agreement between the supposed sensible period of the symmetry-bands proper (diagram C curve 2) and that of the narrowing of the central field (curves 9—14). Kühn & Henke (1936) and Stubbe (1938) have shown that while moderate heating („Wärme") (curves 10 and 12) tends to increase the area of the central field, very strong heating („Hitze") (9, 11, 13 and 14) will cause it to narrow. In all cases the maximum effect occurs at 54 h. a., i. e. exactly at the time at which the maximum increase in the darkening of the ground of the symmetry-bands is supposed to occur in my hypothetic curves. As this hypothesis was constructed independently of the curves showing the variation of the field, I regard this agreement as a strong proof of the correctness of my suppositions.

A necessary consequence of my hypothesis is the supposition that the variation of the shadow follows similar principles. Again we have to consider a longitudinal component (the same as that found in the symmetry-bands) and a transverse one. This last one must be different from that of the other bands, if the so-called „systems" are to vary independently of one another, as shown by Kühn and his collaborators. Thus we have to construct the curve of variation of the shadow as a whole (diagram D curve 17) by adding the curve (1) of the longitudinal design to a new one of the transverse component in the shadow (3). It is evident from the diagram that the resulting curve (17) has almost exactly the same appearance as those found experimentally by Wulkopf (1936). (It may be stated here that the basic-curve was constructed solely to conform with the facts known about the symmetry-bands, the shadow not being considered at all at that time). The curve of the transverse component of the shadow — the shadow proper — must begin at about 12 h. a. if the result wanted is to be arrived at. Consequently, the theoretically strongest effect on the ground in this "system" is attained as early as at 30 h. a., but is, in fact, more distinct a little earlier — as shown by Kühn & Henke 1936 Abb. 87 b (18—24 h. a.) (on account of the interaction with the longitudinal design). In most of the other wings treated at this age the necessary genetical basis for a development of a strong shadow is lacking. The distinct difference between Abb. 87 b and 87 d will be noted, these figures showing a strong development of the ground — an uninterrupted band — in 87 b, but a dissolution into distinct spots in 87 d (36—48 h. a.), where the ground is weakened and the longitudinal design begins to reappear. Thus, the shadow varies, just as might be expected according to my hypothesis.

The arrangement of the marginal spots — one in each of the cells in question — indicates a certain relation to the veins, i. e. to the longitudinal design, although they may not depend directly on that design alone. Perhaps, the spots show a certain tendency to fuse when the insect is treated in early pupal life, whereas, if it is treated a little later in the pupal period — as the opposite reaction — they show a tendency to separate and to overflow the center of the cell in which they lie.

However, the illustrations at hand are not conclusive. In diagram F I have compared the curves (18—21) which show the experimental data concerning the variation of the marginal spots by temperature treatment, with the curve showing the hypothetical influence of the longitudinal design (curve 1).

Similarly, it is impossible at present to throw new light on the variation of the discoid spots through the hypothesis presented here. Their variation as seen in temperature experiments (curves 23—26) is compared with the curve of the longitudinal design in diagram G. It is quite well possible to interpret the curves (23 and 26) given by Wulkopf (1936) as due to the variation of the longitudinal design alone, but I do not regard the known facts as conclusive in this respect. The curves of Stubbe (1938) are unintelligible to me in so far as moderate heat appears to have a negative effect, whereas strong heat has no effect at all.

In the above I have operated arbitrarily on the supposition of complete identity in the shape of the curves for the sensible periods of the different designs. In this way I have tried to show that altogether these curves agree sufficiently well with the empirical facts to be of some value for further research. However, things may turn out to be much more intricate than to be fully illustrated by such simple diagrams, and it may be appropriate to direct attention to some interesting features shown by the curves in question.

As shown in diagram E, the basic curve (represented by curve 1, but curves 2 or 3 may just as well be used) may be divided into two partly overlapping parts indicated in the diagram by thin lines. One of these parts is a symmetrical, simplified curve of dispersion lying above the normal value, whereas the other part is a similar curve lying below this value and somewhat later in time (beginning just at the time when the first part attains its highest value). By addition of these curves, the total "basic-curve" results.

Now, there is a possibility that actually two different processes are implied, one with a positive, the other with a negative effect. If so, it is not necessary to suppose an effect of both of them on every part of the pattern. Some characters may perhaps be influenced by only one or the other of these processes, a supposition which may explain why the breadth of the central-field appears to be susceptible only in the time occupied by the positive part of the curve in question, whereas the negative part of the same curve has no effect on the size of that field (although the strength of the different bands is strongly affected — as mentioned above). A similar view may perhaps be of value for the analysis of the variation of the marginal spots.

Another possibility is that there is no fixed connection between the positive and the negative part of the curves of sensibility. Perhaps the negative part can be displaced in proportion to the positive one if different "systems" or different species are considered. Such detailed speculation is, however, to be postponed until a much larger material is at hand. At present the above-mentioned main lines of explanation may suffice.

To sum up: the main features in the variation caused by temperature-treatment of the pupae of *Ephestia kühniella* may be explained by supposing the existence of a very few, probably only three, susceptible processes, all of which have their labile periods during the first part of the pupal life. These periods succeed one another or overlap in a manner strictly established for each "system". The first of the labile processes appears to influence the longitudinal design, responding to temperature-shocks by a positive reaction (more intense blackening) from the beginning of the pupal stage — or rather from a moment about 6 hours before the pupation — and until about 20 h. a. The negative reaction of the same design occurs in the period 20—72 h. a. The next process to be susceptible is the grund in the shadow band, reacting positively at 12—40 h. a., negatively at 20—92 h. a. Finally, the breadth of the central-field and the blackening of the ground of the symmetry-bands may be altered by treatment at 36—63 h. a.; in this period the bands assume a stronger colour and the field is narrower, whereas in the following period — at about 63—114 h. a. — the bands are paler, whereas the field as such shows no reaction. The notches of the symmetry-bands alter in size, mainly to correspond to the variation of the field, i. e. a broader field is followed by a diminution of the size of the notches.

Consequently, the four "Zeichnungssysteme" erected by Kühn & Henke (1929) for the pattern of *Ephestia kühniella* cannot be regarded as real units, comparable to the designs ("Zeichnungen") on the wings of different Lepidoptera described by Schwanwitsch (1924—35), Süffert (1927—29), Henke (1928—36) and other authors. It must be realized that

1) The system of the symmetry-bands ("Querbindensystem") is a combination of the design of the symmetry-bands and the longitudinal design.

2) The shadow-system ("Schattensystem") is a combination of the shadow-design and the longitudinal design.

3) The marginal spots ("Randfleckensystem") may perhaps be due to a separate marginal design, possibly they are associated with the longitudinal design, but the analysis is very uncertain.

4) Similarly, the discoid spots ("Mittelflecken") may perhaps turn out to be a combination of the longi-

tudinal design and a special, uninfluenced, discoid one — or they may be due to only a single design.

Literature.

As to the literature in general, the readers are referred to the list given at the end of the preceding paper. The papers forming the direct basis of the present treatise are:

Feldotto, W. (1933): Sensible Perioden des Flügelmusters bei *Ephestia kühniella* Zeller. Arch. Entw.mech. 128.

Kühn, A. (1932): Zur Genetik und Entwicklungsphysiologie des Zeichnungsmusters der Schmetterlinge. Nachr. Ges. Wiss. Göttingen VI Biologie 6.

— & M. v. Engelhardt (1933): Ueber die Determination des Symmetriesystems auf dem Vorderflügel von *Ephestia kühniella* Zeller. Arch. Entw.mech. 130.

— & K. Henke (1929—36): Genetische und entwicklungsphysiologische Untersuchungen an der Mehlmotte *Ephestia kühniella* Zeller. I—VII (1929), VIII—XII (1932), XIII—XIV (1936). Abh. Ges. Wiss. Göttingen math-phys. Kl. N.F. 15.

Lemche, H. (1945): The Longitudinal Design in the Wing-Pattern of Lepidoptera, especially in the Fore-Wing of *Ephestia kühniella* Z. (Lep., Pyral.). Entom. Medd. 24.

Stubbe, A. (1938): Die Wirkungen verschiedener Reizung mit erhöhter Temperatur auf das Zeichnungsmuster zweier Stämme der Mehlmotte *Ephestia kühniella* Zeller. Z. ind. Abst. Vererb.-lehre 75.

Wulkopf, H. (1936): Hitze- und Frostreize in ihrer Wirkung auf das Flügelmuster der Mehlmotte *Ephestia kühniella* Zeller. Arch. Entw.mech. 134.
