The Longitudinal Design
in the Wing-Pattern of Lepidoptera,
especially in the Fore-Wing of
Ephestia kühniella Z. (Lep. Pyral.).

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1. Introduction.

The colour-pattern on the wings of the Lepidoptera
has been shown by Schwanwitsch (1924—35), Süf-
fert (1925, 1927, 1929), Kühn (1926), Henke (1928,
1933 a, 1936), Lemche (1937, 1944), Henke & Kruse
(1941) and other scientists to consist of a number of de-
signs varying independently of one another and occur-
ring either alone or — generally — combined.

Schwanwitsch (1929) calls attention to a deficiency
in Süffert's diagram (1927) of the general pattern of
butterflies, which lacks all the elements called venosae
and intervenosae by Schwanwitsch, i. e. all the long-
itudinal components. Later on Süffert (1930) in some
degree makes up for this drawback by including all
the components dependent on the presence of the veins
in a special design under the name of "abhängige Zeich-
nungen". However, the group of German scientists
(Kühn, Henke a. o.) who has worked with such ex-
cellent results on *Ephestia* and other moths appears to
have neglected the presence of this longitudinal design*),
regarding the disturbances caused by the presence of

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*) with the exception of Henke (1936 p. 79).

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the veins in the course and appearance of the transverse designs as a mere matter of fact. Their view may be illustrated by referring to their classification of the pattern-components of *Ephestia*, which are divided into four different "Systeme" (Querbindensystem, Randfleckensystem, Schattensystem, and Mittelflecken), none of which are true longitudinal designs.

In a paper just published (Lemche 1944) I have shown the so-called „Schattensystem" to consist of components influenced in different ways by certain genes. Two of these genes cause variation presumably in the dark spots where the veins cross the shadow-band, whereas a third gene has its more visible effect between the veins. These results — together with some unpublished observations — induced me to make a revisional analysis of the whole pattern of *Ephestia*, going much more in detail than Kühn & Henke (1929) and other authors do in their papers.

Now, the pattern of *Ephestia kühniella* is, in fact, very indistinct, so I soon turned to related species in order to find confirmation of the observations made on *Ephestia*. The results arrived at in this way appeared to be of a more general value, and consequently I extended my studies to other lepidopterous groups. Thus, the paper presented here intends by way of comparison with widely different Lepidoptera to gain a more detailed knowledge of the pattern of *Ephestia,* in so far as the longitudinal components are concerned and, secondly, to study the rules regulating the appearance of that part of the pattern.

Before turning to the detailed analysis it may be useful to discuss briefly the possible causes of the difference between the pattern of the veins and that of the intermediate part of the wing (the "wing-ground" as I propose to term it). This may be done by formulating the three hypotheses theoretically possible:

I. The wing-ground hypothesis: The pattern is supposed to be induced in the wing-ground without the co-operation of the veins, these being included in the pattern simply by "overflowing".

II. The vein hypothesis: The veins are the parts of the wing in which the pattern is developed; from them it spreads to the wing-ground.

III. The independence hypothesis. The pattern develops independently in the veins and in the wing-ground.

Naturally, on setting up these three possibilities against each other it is by no means suggested that one of them should be universally valid, but I am convinced of the importance of bearing in mind in each case whether a special design is associated with the veins (or, let us say, based on the veins) or it is caused by some sort of processes reaching the place directly through the wing-ground, or whether it should be explained by some sort of combination of these possibilities.

The above-mentioned analysis of the genetic basis for the variation of the shadow-system may illustrate this problem. Kühn and his collaborators regard this system as a unity (although made up of several different spots). However, I have found some factors which influence the degree of darkness of the spots, and another one which affects the ground between the spots. The first ones must act — at least partly — through the veins (in a manner totally unknown), the last one appears to reach the shadow independently of the veins.

Thus, we come to the problem whether all the different veins act in exactly the same way, or they respond differently to the determinative processes. For instance, if a transverse band crosses several veins, are then all the spots on the veins similar to each other or are there any laws which make special veins respond in a different way from the rest? Or are some veins

distinctly more „inclined" to show the longitudinal design? These and similar questions are to be treated in the present paper.

However, if the spots on the veins of different moths are to be compared, it is necessary to have a nomenclature fitted for this purpose. The terms introduced by Kühn & Henke (1929) for the pattern of *Ephestia* cannot be used in this way. These authors simply denote the spots in each of their systems by a letter indicating the system, numbering with consecutive indices the individual spots from the anterior to the posterior margin (e. g. S_1, S_2, S_3, S_4 for the spots of the shadow), irrespective of the vein on which they occur. In this way the shadow-spot on m_3 is termed S_1, but in the nearly related *Pempelia ornatella* (fig. 2) similar spots are found on m_1 and m_2 as well. These spots cannot be denoted in a similar way when the third spot has been designated as S_1. Similar difficulties arise in the transverse bands of the symmetry-system, as the vein m_2 is totally absent in *Ephestia* but is well developed in *Pempelia*, where it shows distinct pattern-elements.

To me, the only way out of this dilemma is to introduce terms universally applicable. For similar reasons to those mentioned above, the terms used by Schwanwitsch (1924—35) cannot be generally used either, but it is possible by slightly altering the designations of Kühn & Henke to arrive at serviceable names for all elements, i. e. by keeping the letters of the transverse systems intact, but adding — instead of simple numbers — indices corresponding to the veins in question. As examples may be quoted (with the terms used by Kühn & Henke added in parentheses) S_{m3} (S_1), DI_{a1} (DI_6), DII_{cu1a} (DII_4) etc. The spots on the anterior and posterior margins may be termed in a similar way by adding the indices am (anterior margin) or pm

(posterior margin), e. g. DI_{am} and S_{pm}. Only, the discoid spots cannot be directly included in this terminology, but I can see no reason to alter their names.

Still, it may be difficult to designate the marginal spots or other elements occurring on the wing-ground between the veins, i. e. in the "cells". Schwanwitsch (1924—35) has named such elements by using the name for the vein just behind it, but this procedure is opposed to general usage, most authors designating the cells in insect wings according to the vein in front of them. I prefer, therefore, to follow the latter practice, indicating the marginal spots by the symbol of their system (R, when using the terms of Kühn & Henke) followed by the index of the vein in front of them (e. g. R_{m1} instead of R_2 for the marginal spot between m_1 and m_3 in *Ephestia*). In the case of transverse bands with very distinct spots on the veins, it is often possible to distinguish between the vein-elements and those of the ground; should it be necessary to keep these components separate, this may be done by adding the prefix v (vein) or g (ground), but in most cases such a prefix seems unnecessary.

By the method indicated above it will always be possible to read directly from the symbols the exact place of a certain pattern-element and to compare corresponding elements in different species with minimal trouble, whereas if the terms now current are used, comparative research will be almost impossible. Another advantage of the terms here proposed is the ease with which parallel variation in elements placed on the same vein may be studied. A certain drawback is the slightly more clumsy construction of the terms, but I regard this as inevitable if clarity is to be obtained.
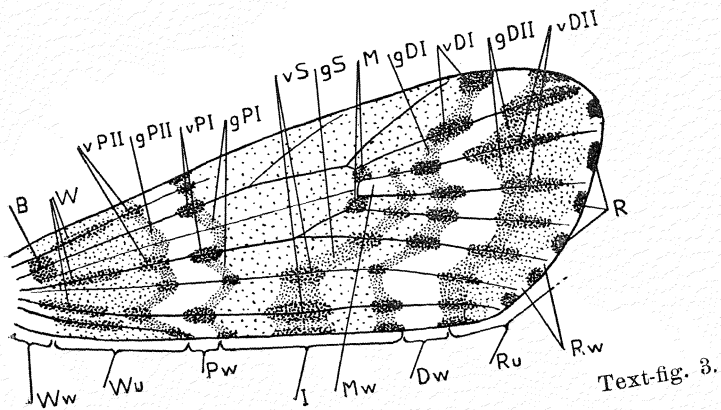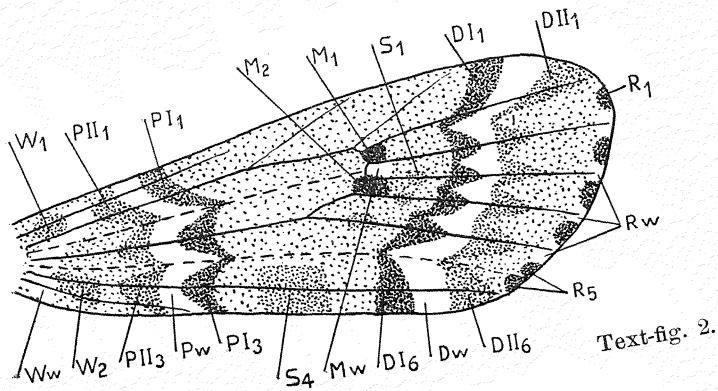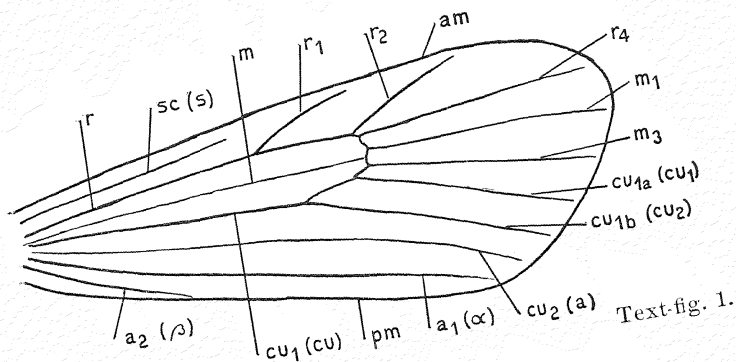
2. The pattern of *Ephestia kühniella* as hitherto described.

The venation of *Ephestia kühniella* is shown in text-fig. 1 with the veins named as done by Comstock & Needham (1898—99) but with the alterations in the cubital and anal region proposed by Tillyard (1919). As Kühn and his collaborators use the original terminology of the former authors, there is a discrepancy as to the cubito-anal region which makes it necessary to add in parentheses the terms used by Kühn. At first sight it might seem of little importance which of these terms are used, but in some earlier papers (Lemche 1935, 1937) the design of the transverse bands in Lepidoptera has been shown to be homologous with that of other insects and to depend in some respects on the veins. Accordingly, it may be of some importance to know exactly which vein is crossed by a certain band

Text-fig. 1. Diagram showing the venation in the fore-wing of *Ephestia kühniella*. (If different, the interpretation of the veins used by Kühn and his collaborators is added in parentheses). a_1 and a_2 anal veins. *am* anterior margin. cu_1 and cu_2 cubital veins. *m*, m_1 and m_3 medial veins. *pm* posterior margin. *r*, r_1, r_2 and r_4 radial veins. *sc* subcosta.

Text-fig. 2. Diagram of the colour-pattern on the fore-wing of *Ephestia kühniella* according to Kühn and his collaborators (based on the records of Kühn & Henke 1929, Köhler 1932, Henke 1933 and Hügel 1933) (for explanation of the letters, vide text-fig. 3).

Text-fig. 3. Diagram of the colour-pattern on the fore-wing of *Ephestia kühniella* according to the view advocated in the present paper. *B* basal spot. *DI* and *DII* dark distal bands. *Dw* white distal band. *g* prefix indicating ground elements. *I* the central field and its bordering bands. *M* discoid spots. *Mw* discoid white spot. *PI* and *PII* dark proximal bands. *Pw* white proximal band. *R* marginal spots. *Ru* marginal field. *Rw* white marginal spots. *S* shadow. *v* prefix indicating venous elements. *W* root band. *Wu* root field. *Ww* white band proximal to *W*.

m r$_1$ r$_2$ am r$_4$

r sc (s) m$_1$

m$_3$

cu$_{1a}$ (cu$_1$)

cu$_{1b}$ (cu$_2$)

a$_2$ (β) cu$_1$ (cu) pm a$_1$ (α) cu$_2$ (a) Text-fig. 1.

M$_2$ M$_1$ S$_1$ DI$_1$ DII$_1$

W$_1$ PII$_1$ PI$_1$ R$_1$

Rw

R$_5$

Ww W$_2$ PII$_3$ Pw PI$_3$ S$_4$ Mw DI$_6$ Dw DII$_6$ Text-fig. 2.

vS gS M gDI vDI gDII vDII

vPII gPII vPI gPI

B W R

Rw

Ww Wu Pw I Mw Dw Ru Rw Text-fig. 3.

in each separate place, and this knowledge depends in its turn on the correct opinion as to the homologies of the venation of different insects. This is the reason why I have not simply followed the terminology used by Kühn and his collaborators.

Kühn & Henke (1929) divide the pattern of *Ephestia* into four "systems", each of which includes all the components supposed to vary parallelly, but independently of those of the other systems. The diagram of the pattern given by these authors is redrawn in textfig. 2 — with some alterations and additions given in later papers by Kühn and his collaborators. At the points where the veins m_1 and m_3 spring from the discoid vein we find two small black spots, the discoid spots ("Mittelflecken", M_1 and M_2). Hügel (1933) adds a white element (M_w) between these two spots. These components constitute a system of their own; they are placed in the middle of a larger area, the central field ("Zentralfeld") bounded distally and proximally by transverse bands which are termed the distal band ("Distalbinde") and the proximal band ("Proximalbinde"). Each of these bands consists of three slender bands, viz. a very dark one bordering the central field (DI resp. PI), a white median part (Dw resp. Pw), and a darker band (DII resp. PII). Each of the slender dark bands are considered to be composed of a number of arrow-shaped spots placed above the veins crossing the bands. The middle of the central field may be regarded as an axis of symmetry (hence the said bands may be designated as "symmetry bands"), and thus the outer distal band and the inner proximal one may be said to lie axifugally to the rest of these bands. Still more axifugally two lighter areas are found, one proximally, the other distally on the wing; these areas are regarded as "Umfelder" in the sense of Henke (1933). All these components (exclusive of the above-mentioned discoid spots) compose the system of

the transverse bands or the symmetry system. Between
the veins along the outer margin of the wing the mar-
ginal spots ("Randflecken", R_1-R_5) constitute a third sy-
stem, and finally, in the outer and hind part of the
central field, there occur some more or less distinct
spots arranged in a transverse row, the shadow system
("Schattensystem", S_1-S_4). Henke (1933) on the basis of
observations published by Köhler (1932), adds two root-
spots ("Wurzelflecken", W_1 and W_2) near the base of
the wing, and the same author gives the marginal spot
R_5 a different shape, indicating a partial splitting into
two. Finally, Hügel (1933) adds some white spots along
the outer margin between the dark marginal spots.

During my study of the pattern of *Ephestia* I ar-
rived at a somewhat different opinion as to the arran-
gement of the elements of the pattern, the reasons for
which are given below. My view is illustrated in text-
fig. 3, in which the terminology proposed above is
used.

3. The pattern components of the wing base.

In several geometrid moths Henke (1928, 1933) has
found a root-band ("Wurzelkern") corresponding to and
varying parallelly to the symmetry-system of the middle
of the wing. This root-band has not hitherto been shown
to exist in *Ephestia*, but, as mentioned by Henke &
Kruse (1941), the basal part of the wing (proximal to
PII) no doubt contains more dark pattern-elements than
those described by Köhler (1932) as the "Wurzel-
flecken" W_1 and W_2. Köhler's interpretation is based
on the arrangement of the differential mitoses in the
pupal wing and appears to be imperfect. He places one
spot near the anterior margin very near the base of
the wing, and the other (W_2) proximal to PII_3 (cf. text-
fig. 2). Moreover, he mentions a white spot distal to W_1
and a somewhat larger white area proximal to W_2. The

strange feature that the dark and white spots lie inversely in the two cases, however, appears to me to indicate that his interpretation needs some correction.

In some of my stocks of *Ephestia kühniella* which show a strongly developed shadow, the basal part of the wing possesses very distinct pattern elements, which could be studied in more detail than usual when the wing was removed from the body with special care. In these wings dark pattern components are present as longitudinal streaks running from near PII almost to the base of the wing along the veins sc, cu, a_1 and a_2 (figs. 4, 5, and text-fig. 3). The elements of the two anal veins often fuse so as to form a broader spot (fig. 5), which at first sight appears to belong to the vein a_1 but is placed obliquely above that vein. I did not understand the arrangement of this spot until I realized the part played by the vein a_2 in the development of it. It appears that this spot is termed W_2 by Köhler (1932). In the closely related *Pempelia ornatella* the second anal vein shows pattern elements throughout its whole extent (fig. 2, a_2), once more illustrating the part played by this very small vein in the development of the pattern. It is very curious that in *Ephestia* the element on the radius is totally lacking, just as is the corresponding element of PII, although this vein is very marked, whereas some slight traces of a spot are present on the very faintly developed cu_2 ("Analis" of Kühn a. o.).

All these elements constitute a broad, interrupted root-band (W), which runs across the wing proximal to PII, often fusing distally with this last band, but no doubt to be regarded as a separate pattern component.

Finally, the innermost parts of the root-elements on the subcosta and the cubitus are united by a quadrangular spot, the relation of which to the root-elements appears to be uncertain. At present, I prefer to regard it

as a separate element, the basal spot (fig. 4, B), corresponding to Köhler's W_1 (1932).

A comparison with *Pempelia ornatella* (fig. 2) confirms the interpretation of most of the basal pattern components. Here, there are distinct root elements on sc, cu_1, a_1 and a_2 (these last partly fused), and slight indications of an element on cu_2. Moreover, in this species the difference between the greyish root-elements and the black PII is very obvious. Only the basal spot is very indistinct.

The foremost part of the white W_W of Köhler comes to lie in the middle of the root-band, viz. in the area around the radius, which, as mentioned above, lacks a dark root-element. This light spot is, however, inconspicuous even in very strongly coloured stocks and can hardly be regarded as a distinct element at all. On the contrary, the hindmost part of W_W is much lighter coloured than its surroundings, though hardly as bright white as P_W and D_W. This part of the "Wurzelfleck" of Köhler may, therefore, be regarded as a distinct element and we may retain the designation W_W for it, but the whole of it is placed proximal to the root-band.

In an earlier paper (Lemche 1937, pag. 248 fig. 2) I have compared Henke's (1928, 1933) diagrams of the patterns of geometrid and pyralid moths with my diagram of more primitive Lepidoptera, but this comparison has been opposed to some extent by Henke & Kruse (1941). Their objection is mainly based on a misunderstanding owing to the presence of some elements — in this respect of no importance — which are indicated in one of Henke's diagrams. Thus, a more precise statement of my view seems to be in place.

The symmetry-system constituted by the transverse bands is found on the wings of most Lepidoptera, but while there are several bands in primitive types, most of the members of the more specialized groups show a

single very broad band, just as in *Ephestia*, or in some
cases one more band proximal to the largest one. Now,
for various reasons I suppose the broadest band to be
the third one of primitive moths when counted from
the base of the wing, whereas the two innermost ones
have partly — or totally — disappeared. Unfortunately
the second band in my diagram has accidentally been
placed exactly above the interspace between the two
bands present in Henke's diagram, and this has caused
Henke & Kruse to interpret my diagrams as if I
homologize the second band with a slightly indicated
element (the "innere Hauptbinde") of a quite different
origin lying in the said interspace. However, such darker
components in the interspaces between the bands have
been observed by me in Tortricids without being inter-
preted as true bands, and Henke & Kruse's supposi-
tion concerning my view is incorrect. My interest at
that time was directed towards the question of what had
been the fate of the two bands originally present prox-
imal to the broadest one — as discussed in some detail
in the paper in question (Lemche 1937 p. 250). Thus,
the remarks of Henke & Kruse (1941 p. 174) concern-
ing the interrelations of the different pattern components
are not in opposition to my conception of the homologies
of the primitive bands in the higher Lepidoptera.

As to the pattern of the basal part of the fore-wing
of *Ephestia*, Henke & Kruse (1941) suppose the ex-
istence of the outer half of a "Wurzelkern", given in
their diagram as a basal white band and, distal to it,
a darker one. This view fits very well with the inter-
pretation given above, which is based on observations
made several years ago. The root-band described above
may therefore be regarded as the outer border of a sepa-
rate "Kern" in the actual base of the wing of *Ephestia*.

4. The shadow.

Kühn & Henke (1929) give the shadow as consisting of four separate spots (viz. on the veins m_3, cu_1, cu_2 and $\asymp$ in their terminology). In later papers — especially after the investigation on the shadow-system by Clausen (1937) — Kühn appears to be more inclined to regard it as a band which extends across the greater part of the wing and develops darker spots on the veins. This view is confirmed by my own results (Lemche 1944), since there has proved to be at least one gene which develops a distinct darkening of the intervenous spaces between the spots, giving the whole system the appearance of an uninterrupted band. In that paper I used Kühn & Henke's terms for the different spots, having done most of that work more than twelwe years ago, at a time when the present paper had not yet been planned.

Süffert (1927) and Henke (1928) mention for some geometrid moths a "Mittelschatten" running as a transverse band across the wing between the two bands of the symmetry-system, and Henke shows this "Mittelschatten" to vary independently of these other bands. It seems probable that the shadow of *Ephestia* may be homologous with the "Mittelschatten" (a possibility already realized by Kühn & Henke 1929), but there is a certain difference, since on the wings of Geometrids the "Mittelschatten" extends forward to the front margin or at least to the last radial vein, whereas the S_1 of Kühn & Henke in *Ephestia* is placed on m_3. In the pyralid moth *Phycita spissicella* (fig. 1) the shadow appears as a row of distinct spots darker than any part of the symmetry-system and it is, consequently, easy to follow throughout its whole course. In this species, m_1 possesses a distinct shadow-spot (S_{m1}) touching distally the corresponding element in the distal band (DI_{m1}). Precisely the same appears to be the case in another

Pyralid, *Pempelia ornatella* (fig. 2), but in that species the distal band is similar in shade to that of the shadow, and hence it is very difficult to distinguish with certainty between the elements in question. In none of these species does any radial vein show traces of the shadow. Contrary to *Ephestia*, both species have a distinct vein m_2, and a distinct shadow spot is developed thereon (S_{m2}). Now, it may be supposed that a spot S_{m1} exists in *Ephestia* too, and it is actually visible on some wings in this species, where it may be almost entirely separated from the corresponding spot on the distal band (fig. 3). Similarly, it is visible in some figures given by Köhler (1932, Abb. 59, 80h, 89) illustrating the development of the pattern in the pupa.

These examples may suffice to show that in Pyralids — and among them *Ephestia kühniella* — the shadow is a band which extends across the whole wing except the foremost part occupied by the radius, just as the "Mittelschatten" in some geometrid moths (Henke 1928, Abb. 6 b, c). Moreover, the number of spots in the shadow of *Ephestia* exceeds four.

Turning now to the internal structure of the shadow, it has been possible (Lemche 1944) to show the existence of certain genes which influence separately either the spots on the veins or the wing-ground in the cells between them. For details I refer the reader to the paper just cited; it will suffice here to illustrate the results by means of two figures showing the possibility to find different strains which have a similar total number of dark scales in the shadow, but differ in the arrangement thereof, one of the strains possessing strong spots on the veins (vS) but no or few dark scales in the interspaces (gS) (fig. 6), the other having shadow-spots hardly distinguishable from the interspaces (fig. 7). This means that within a single system (in the sense of Kühn and his collaborators) the ground colour varies

independently of the venous spots, and the points of
intersection between a transverse band and the veins
cannot simply be regarded as centres for the diffusion
of pigments (or pigment-inductors). On the contrary,
the ground between the spots has a threshold
value of its own for pigmentation, which is
independent (at least partly) of the threshold
value of the spots themselves.

5. The general influence of the veins on the transverse designs.

If the results arrived at in the above are correct,
they may be valid also for other transverse systems
on the wings. Here the symmetrical bands are of pri-
mary importance on account of their detailed differentia-
tion. Now, features comparable to those described for
the shadow are more easily recognized in the distal
band, although PI also to some extent shows a differ-
ence between the spots on the veins and the darkened
ground. In fig. 8 this difference is especially distinct
in DI, the spots of which are quite black, whereas the
colour of the intermediate part of the band is only grey-
ish. Kühn & Henke (1929) in their Tafel I give an
excellent drawing of the outer part of a wing, showing
with great clarity the bands DI and DII to consist of
continuous bands of greyish "Uebergangsschuppen",
whereas the "dunkle Zeichnungsschuppen" are localized
on the veins. This phenomenon is most readily seen in
the spots DI_4 and DII_3 in that figure, but it is also
very distinct in other parts of it. It appears that we
are not dealing with "Pfeilflecken", but with narrow,
dark zones along the veins, which intersect the dark
greyish transverse bands of the ground. By keeping
strains under controlled conditions during several gene-
rations, the pigmentation of the spots has been found to
vary independently of that of the ground, as shown in

'figs. 9 and 10 for band DII. Both strains have very small, but distinct, spots on the wings, but while the strain in fig. 9 has no darkening of the ground, such a pigmentation is very distinct in the other strain shown in fig. 10. A comparison of the two figures, 8 and 9, reveals the same feature for band DI (and PI). However, the pattern of *Ephestia* is far too indistinct to be a fit object for a general study of the relation between the venous spots and the interspaces, and a comparison with other species appears to be much needed.

Some stocks of *Ephestia* show a pattern which is distinctly associated with the veins (fig. 11) though the general appearance of the pattern is only little altered. Still more conspicuous is the dependence on the veins in *Pempelia ornatella* (fig. 2), but this appearance may here be due to a lack of pattern-bearing scales in the cells between the veins, and, this being the case, the difference is not one of pattern but is due to developmental processes regulating the arrangement of the scales. (Of course, even in this case it illustrates a difference between an area covering the veins and an intermediate area). In such cases it is possible to imagine the veins being the only bearers of the pattern-causing impulses, but large numbers of species which show distinct differences between the veins and the ground may be enumerated. It will suffice here to refer to the three species *Aporia crataegi* (fig. 14) with a purely venous pattern, *Papilio podalirius* (fig. 15) with no darkening at all on the veins but with distinct transverse components, and *Papilio machaon* (fig. 16), which shows a combination of both. In *Aporia crataegi* and *Papilio machaon* the dark scales are distributed along the veins; in the first case they show no distinct pattern except the longitudinal one, but in other cases, e. g. in *Biston zonarius* (fig. 17), the veins and the ground respond independently to the pattern-inducing impulses in the way known from

Ephestia. In *Biston,* the veins as well as the ground show the tranverse designs, but the intensity of the colouring is highly different, the veins bearing much darker scales than those of the ground, just as in some specimens of *Ephestia* (cf. fig. 8).

As to the two cases mentioned it may be objected that there is only a single point of difference between the two parts of the pattern, viz. that the veins are always darker than the cells. However, the complete independence of the ground may be illustrated by comparing the two species *Hadena monoglypha* (fig. 18) and *Hadena lithoxylea* (fig. 19). The venous patterns of these two species are almost identical (cf. DI and DII in the two wings), whereas the ground patterns are very different in strength.

In some species the pattern elements on the veins are placed side by side with those of the ground, as seen in the distal band of *Ephestia* (fig. 8), etc., but in other species the venous elements are displaced axifugally in relation to the corresponding ground elements of the symmetry system. This is well illustrated in *Hadena monoglypha* (fig. 18), in which the distal band is placed distinctly more axifugally on the veins than on the ground; further it is seen in *Codonia annulata* (fig. 20) and *Lymantria monacha* (fig. 21) and many other moths in a slightly modified fashion, the bands running across the wing having distinct axifugally directed points for every vein, the intermediate parts forming axipetal curves. In such cases the veins appear to have acted as funnels through which the pattern-inducing impulse has spread more easily than through the ground itself. Contrary to this, some species show outward-facing curves in the interspaces (*Cidaria truncata,* fig. 22).

The examples mentioned above may suffice to show that the veins and the intervenous spaces, the "cells", react independently on the pattern-causing processes.

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Furthermore, Schwanwitsch (1929) mentions for the genus *Satyrus* a reduction of the row of eye-spots, the second and fifth of which are very stable, whereas the other spots tend to disappear. In *Catagramma* (Schwanwitsch 1930) the second, third, and sixth spots are the more stable. Thus, the different cells vary in their ability to respond to the eye-spot-causing impulses and are independent of one another, although the relative arrangement of the pattern-components is the same in all the cells. Precisely the same may be said for the veins: in *Lymantria monacha* (fig. 21) the distal band DI extends nearly as close to the margin on the veins cu_{1a} and cu_{1b} as on m_3, whereas in *Cidaria truncata* (fig. 22) the component on m_3 lies far more distally than those on the other veins mentioned.

6. The pattern-inducing effect of the anterior and the posterior margin.

The anterior margin of the wing is supported basally by a true vein, the costa, but along most of its course — similarly to the posterior margin — it lacks the trachea characteristic of true veins. However, blood-spaces occur in the margins of the wing, and consequently it may be of some interest to go into the question whether distinct pattern elements are detectable on the margins. Now, the investigations of Behrends (1935) and Köhler (1940) have shown the tracheae to be of no influence on the pattern, as they undergo several modifications during the pupal life which are not traceable in the final colour-pattern, and — moreover — some of these tracheae may be lacking in the pupal wing without this altering the normal pattern of the imago.

When, however, the tracheae have no influence on the pattern, there appears to be little difference between normal veins and the wing margins. Hence, it is not surprising to find well developed pattern elements on

the margins corresponding in every respect to those on the veins. A close study of the wings of *Ephestia kühniella* revealed that in some cases the apparent spot DI_{r4} is divided into a semicircular spot on the anterior margin and an elongated spot on r_4 (figs. 5, 12). Generally, these two spots fuse so as to form one of a characteristic shape (fig. 13). In a similar way DII_{r4} may show a splitting of its proximal part (fig. 12), but lying very near the margin, it cannot be totally separated into two. The posterior margin sometimes shows the same reaction to the presence of the distal bands in such a way that a distinct narrowing is seen between the elements on a_1 and on the margin (figs. 4, 11). Moreover, the shadow behaves in a similar manner, the spot designated by Kühn and his collaborators as S_4 containing three elements (text-fig. 3 and figs. 10, 11), one of which is placed on the posterior margin and one on a_1 (as for the part played by cu_2 see below).

However, the whole pattern is so indistinct in *Ephestia* that it seems desirable to corroborate the interpretation by way of a more favourable object. In *Pempelia ornatella* (fig. 2) the effect of the hind margin appears to be indisputable, though the pattern-bearing area is very narrow. The alternation of dark and light groups of scales cannot be explained in any other way (in the photograph it is much less distinct than on the object itself). In this connection it may be worth mentioning that displacements ("pierellisation" or "Verwerfungen") may occur along the margins (Henke 1933) as well as along the normal veins (Schwanwitsch 1928, Süffert 1927). The front margin in *Pempelia* is not of the same interest, as the whole of the wing-area in front of the radius is covered by pattern-bearing scales, which obscure the borders of the different spots in the same manner as in *Ephestia*.

In *Pempelia* a distinct area along the outer margin

is furnished with white and black scales in the same way as the hind margin — but much more pronounced — corresponding to the presence of a marginal blood-space. The veins running to the outer margin cause a rhytmical variation in the colour, but in all other respects the outer margin appears to behave as a true vein as regards its influence on the pattern.

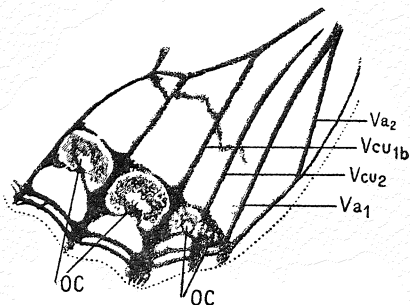## 7. The influence of the "weak" veins on the pattern.

We are now confronted with the question whether special veins generally tend to influence the pattern in another way than the remaining ones.

Turning first to our main object, *Ephestia kühniella,* we find that Kühn & Henke (1929) describe five marginal spots, viz. one (R_1) in the cell behind the vein r_4, and further a spot in each of the next four cells behind, the last one (R_5) lying in the cell between cu_{1b} (cu_2 of these authors) and a_1 ($\propto$). However, R_1 is very rarely distinct, being often included in the very large element DII_{r4} (fig. 9, R_{r4}) or having disappeared altogether (fig. 12), but still five marginal spots are often clearly visible. Moreover, when the first spot is present, it is sometimes possible, or even very easy, to count six distinct spots (cf. Kühn & Engelhardt 1933 Abb. 12 l). This fact has also been realized by Feldotto (1933 p. 305), who writes: "In seltenen Fällen ist - - - ein 6. Randfleck zu beobachten. Dieser liegt zwischen c_2 und $\propto$ hinter R_5. Gewöhnlich geht er in DII_6 auf. Dass zwischen den beiden Adern c_2 und $\propto$ zwei Randflecken vorhanden sind, ist nach der Entwicklung des Flügels gut verständlich". In spite of this observation, the diagram has not been altered correspondingly in later publications by Kühn and his collaborators, with the exception of that of Henke (1933), who gives the fifth marginal spot as partly divided, though not totally separated, into two. However, the presence of the sixth spot is far too com-

mon to allow us to disregard it in this way, and hence my diagram (text-fig. 3) contains all the six spots.

Schwanwitsch, in several of his papers holds a similar view. On discussing the genus *Melanargia* (Schwanwitsch (1931)) he describes very carefully the pattern in the "first cell" (i. e. the cell between cu_{1b} and a_1, Schwanwitsch counting the cells from behind). In this cell there are two eye-spots instead of the single one found in his prototype. The distinctness of the two spots varies within the genus, the hindmost one often being more or less rudimentary (cf. text-fig. 4). Now, there are also typical black stripes along the veins, on cu_{1a} and cu_{1b} as well as on the first and second anal veins. Schwanwitsch, however, mentions and figures a "1st intervenosa" lying ex-

Text-fig. 4. Part of the hind-wing of a member of the genus *Melanargia* showing a typical venous pattern-element on cu_2, and the doubling of the eye-spot caused by the presence of that "weak" vein. Va_1, Va_2, Vcu_{1b}, Vcu_2 venous pattern-elements. OC eye-spots. (After Schwanwitsch 1931 — letters altered).

actly along the "rudimentary" cu_2. None of the other intervenosae being present, it appears to me to be much simpler to interpret the dark "1st intervenosa" as a true venosa, viz. the longitudinal component on cu_2. More-over, the same component continues to the margin ex-actly in the tract which divides the two ocellar spots of the "first cell". The whole appearance of the pattern points towards the view that the vein cu_2 is not rudi-mentary in so far as it has a distinct influence on the

development of the pattern, the longitudinal design as well as the eye spots.

When, therefore, Schwanwitsch (1930 p. 297) says that "--- the eye-spot in the 1'st cell is duplicated which is generally a common thing in nymphaloids", it should be realized that the "cell" between cu_{1b} and a_1 consists of two separate cells, one behind cu_{1b} and one behind the "weak" vein cu_2. Schwanwitsch's prototype should be altered accordingly, so that two separate eye-spots are indicated in that region, one in front of and one behind the vein cu_2. When in some cases only one eye-spot is present, this may be taken to be due to reduction, just as is the case with other components in the pattern.

I do not hesitate to interpret the conditions found on the wing of *Ephestia* in the same way. The marginal spot R_5 of Kühn & Henke should be divided into two distinct spots, R_{cu1b} and R_{cu2}. Kühn & Henke (1929) appear to have only taken the strong veins easily seen in the imaginal wing into consideration, and to have forgotten the possibility of an influence caused by cu_2 (their "a"), which disappears during the pupal life. (Later on, it has been shown by Kühn and his collaborators that the spots must be induced at least very early in the pupal life — if not even a little before. — The vein cu_2, however, is reduced at the same time or a little later (Behrends 1935), and consequently it may very well be supposed to have some influence on the pattern.)

If cu_2 has actually the effect supposed in the above, we must expect that it exerts an influence on other parts of the pattern, also, and this has indeed proved to be the case. In band DII of *Ephestia* there is a distinct spot on cu_2 in many wings (fig. 5 — and less distinct in figs. 3, 4, 8 and 11), whereas the spot DI_{cu2} (figs. 5, 13) is more rarely found, and if present it is always

much smaller than the other elements of DI. In the proximal and root bands the corresponding elements are never represented by more than a few scales, whereas the shadow sometimes has a distinct element on cu_2 (fig. 9). However, this element tends to fuse with that on a_1 and on the posterior margin forming the large spot designated by Kühn & Henke (1929) as "S_4". Thus, the effect of the "weak" vein cu_2 is distinct in the marginal spots, DII and the shadow, faint in DI, and lacking in PI, PII and W.

Turning now to other Lepidoptera, looking for similar evidence of the effect of "weak" veins, we may mention the pattern of *Pempelia ornatella* (fig. 2), which shows cu_2 to be covered with a stripe of pattern-bearing scales comparable to those of the other veins though much thinner, its white parts being nearly indistinguishable from the ground scales on both sides. In this species — in contrast to *Ephestia* — also the proximal parts of the pattern are represented on that vein. Similar conditions are found in the bombycid moth *Odontosia carmelita* (fig. 23), in which the components on cu_2 are almost as strong as those on the other veins. However, *Aporia crataegi* (fig. 14) lacks even the slightest trace of similar pattern-elements, though the place of the vein itself is distinctly visible as a slight furrow. In fact, it is possible to find every transition between species which show no effect at all of that vein, and such as have nearly just as distinct pattern-elements on this as on all other veins (e. g. *Lymantria monacha*, fig. 21). The influence on the marginal spots is characterized by the separation of the two spots in question, whereas a less effect causes them to approach (*Acronycta psi*, fig. 24, R_{cu1b}, R_{cu2}), until finally they totally fuse (*Luperina hawor-thii*, fig. 30, R_{cu1b}).

A very interesting fact is that cu_2 has not always a less effect than the other veins. On the contrary, it

has in several cases a special influence differing from that of the normal veins. This is well illustrated in the species of *Acronycta,* which have often a strong black stripe along the inner third of cu_2, and again on the outer third (cfr. *Acronycta psi,* fig. 24, V_{cu2}); these long-itudinal components have no homologues on the other veins. The same feature is much more conspicuous in *Acronycta alni* (fig. 25), which has a totally melanistic cu_2, whereas the other veins are very light in colour. Generally, *Miana bicoloria* (fig. 26) has no special com-ponent on cu_2, but in some specimens from the west coast of southern Jylland (fig. 27), kindly placed at my disposal by Mr. N. L. Wolff, the wing is melanized over cu_2 in just the same manner as in *Acronycta alni,* even though the remaining surface of the wing is of almost the usual appearance. Similarly, in *Diloba coeru-leocephala* (fig. 28) a longitudinal streak on cu_2 is seen in the distal part of the wing. Thus it proves possible for cu_2 to exert an influence on its pattern in a very vari-able way independently of the other veins, and examples of a similar kind may easily be obtained.

In *Taeniocampa munda,* the only distinct pattern elements on the normal wing are two close-set, dark spots in the distal part of the median area, but in a single specimen I have found two more spots lying each on its side of the outer part of cu_2 (fig. 29, X_{cu}). Just as those on the media (X_m), they appear to belong to the components termed "unechte Randflecken" by H e n k e & K r u s e (1941). Other species of *Taeniocampa (gothica* L. and *incerta* Hfn.) show more or less slight indications of the same tendency to increase the darkness of the corresponding band in the places mentioned. The strange parallelism between the media and the cubitus will be discussed below; here it will suffice to state that cu_2 appears as a vein whose influence on the pattern is more or less independent of that of the other veins.

This feature, however, is not true of that single vein only. In *Luperina haworthii*, many specimens have a distinct white colour along the branches of cu_1 and the media (fig. 30), which is most conspicuous on m_3 and cu_{1a}, whereas the veins in the foremost part of the wing lack white scales. In other specimens the white colour is very indistint or — on some veins — has entirely disappeared except in the discoid spot. In this species the media and the cubitus behave in quite a different way from the radius. Consequently we may state that e a c h vein is able to change its pattern independ-ently of other veins. This ability is especially well illustrated by the second cubitus, which differs in structure, also.

The problem now arises whether the deviation of the pattern on cu_2 is due to a degeneration of that vein during the late development or it is to be explained in another way. It is generally assumed (cf. i. a. K ö h l e r 1932) that cu_2 degenerates early in the pupal life when its blood-space disappears, only the trachea continuing to exist. It is precisely in this period that the differential mitoses take place and the pattern is labile for tempera-ture-shocks, and consequently the deviating influence of cu_2 on the pattern may be assumed to be due to de-generation.

Unfortunately, the problem is not so simple. On the pupa of *Pieris brassicae* (fig. 32) the marginal spots of the fore-wing behave in precisely the same manner as in the species of *Acronycta* mentioned above (fig. 24), lying each in its cell except around cu_2, where there are two smaller, more closely set spots, one in front of and one behind that vein. Cu_2 is slightly indicated in the imaginal wing of that species in just the usual manner (more easily seen on its under side), and in *Pieris napi* L. the same vein has a distinct longitudinal

streak on its under side similar to that of the other veins in that species. Hence there is not the slightest reason to suppose that in *P. brassicae* cu_2 is reduced a moult before usual, a necessary supposition if the phenomenon is to be explained in the same way as when it occurs on imaginal wings. Of course, if the vein degenerates during the determination of the pattern of the pupal wing (i. e. during the last larval instar or perhaps even before), it cannot degenerate once more while the pattern of the imago is being determined.

The same problem is illustrated in a different way by the frequent feature that some vein or other is present in the wing of a species but is totally lacking in nearly related ones. *Pempelia ornatella* and many other pyralids possess the usual three medial branches, whereas m_2 has totally disappeared in *Ephestia kühniella* (text-fig. 1), though the "degenerated" cu_2 is equally well developed in both. Similar examples may easily be obtained, and in such cases we never find the vein in question in a rudimentary stage; on the contrary, either the vein has fully developed, or it has totally disappeared.

From this it follows that the vein cu_2 cannot simply be regarded as rudimentary; it is an independent vein, differing structurally as well as in its relation to the colour-pattern from the other veins. It functions in the wing in its own characteristic way, whether during the formation of the pupa or of the imago.

Now, the lepidopterous wing contains one more vein which behaves in a similar manner, viz. the inner part of the media. Just as in the case of cu_2, it may lack every trace of a colour-pattern or it may have a very distinct colouring. E. g. in *Biston zonarius* (fig. 17) there is a distinct blackening of that part of the media which lies within the discoid cell (vm), and the same is true of *Odontosia carmelita* (fig. 23). The same feature is seen

very distinctly in *Sphinx ligustri* (fig. 33), in which the outer part of the (here two-branched) media-stem and also m_2 is much more blackish than any other vein except cu_2 (the blackening in the middle of some of the cells is of no importance in this connection). A very curious fact is the colouring not only of the weak part of the vein, but of parts of the distal medial veins, too, owing to which the pattern in the distal part of the medial area shows distinct similarities to that of cu_2.

Such similarities are found in a large number of Lepidoptera. Most striking is the above-mentioned case of *Taeniocampa munda*, which normally has only two close-set, black spots in the medial area on the light brownish wing, but in at least one case (fig. 29) shows two similar spots around the outer part of cu_2. In *Hadena strigilis* (fig. 34) a blackening of the wing not found in other areas is found in the corresponding places. In *Amphipyra pyramidea* L. there is a broad, black, longitudinal stripe through most of the medial area, and a narrower stripe extends along cu_2. The markings characteristic of the noctuid moths are likewise placed on the media (within or at the end of the discoid cell) or on cu_2. In some species of *Acronycta* a faint longitudinal streak intersects the black outer band in the outer medial area, and a similar but much stronger streak occurs in the outer area of cu_2 (but in this case conditions are less easily understood, as the medial streak lies between the veins and not along one of them as in the case of cu_2). The same problem has been discussed by H e n k e (1936 p. 34), who calls attention to two white streaks along the same veins in *Usta wallengreni* Feld.

Not only the strength of the pattern-components vary parallelly in these two areas, but also the place of the pattern may be influenced by these veins in a different way than by any others. In *Ephestia kühniella*, the distal bands show two axipetally directed curves, viz. a

larger one in the medial area and a smaller one at cu_2. Similar curves may be found in the proximal bands (figs. 4, 12, 13). These curves are seen still more distinctly in a specimen of another pyralid, *Aglossa pinguinalis* (fig. 35), but here the cubital curve is the larger one. In this specimen, the curves on PI are very distinct and confirm the interpretation of the corresponding ones in *Ephestia*.

Many other moths show similar curves; in *Codonia annulata* (fig. 20) they are distinct in the proximal band, though they are only slightly indicated in the distal one. In a number of different geometrids the said curves appear as constrictions on the "central field" between the proximal and the distal bands. This is well displayed in *Ortholitha sagittata* (fig. 36, m and cu_2) and is still more evident in *Chesias legatella* (*spartiata* Fuessl.). In most wings of this last-mentioned species, the central field is entirely divided by the media and cu_2 in such a way that an isolated area of that field is found in the middle of the wing (fig. 37). In a single specimen I have found a connection between the hind and the middle part of the central field, but even then this connecting part is much narrower than the rest of the field (fig. 38).

It is not always the weak veins alone which tend to cut the central field into pieces. It may be the case of most other veins, too, as it is seen in *Cidaria truncata* (fig. 22) and many other geometrids. Furthermore, the opposite may be the case, the veins being the places where the central field attains its largest width, as in *Lymantria monacha* (fig. 21) and in *Codonia annulata* (fig. 20), but even in such cases the area around the weak veins may tend to show a decrease in the width of the central field, as is distinctly seen in *Lymantria monacha* (fig. 21).

In general we may say that the cutting into pieces

of the central field takes place principally along the
weak veins, in most cases more markedly along cu₂ than
along the media. In many moths this cutting is indicat-
ed only by a dark streak across the middle part of cu₂
where the dark borders of the fore- and the hind-part
of the central field touch one another (vide e. g. *Hadena
lithoxylea,* fig. 19).

8. The concept of „weak veins" and current hypotheses on the development of the wing pattern.

Henke (1933 b) in his experiments on *Philosamia
cynthia* shows that local destruction on the wing-pads
may alter the final distribution of the central field,
which appears to be more contracted than normally.
He establishes the law that a diminution of the field
causes an increase in "Geschlossenheit" in so far as it
contracts around a centre in the neighbourhood of the
discoid field, becoming at the same time circular just
as the discoid spot. However, the above-mentioned con-
ditions normal to *Chesias legatella* show that this ex-
planation is insufficient, since the contraction of the
central field in this case will result in its being cut
into pieces. Just the same feature appeared in some
experiments made by Kühn & Engelhardt (1933,
Abb. 11 e, p. 682) and has been discussed by me in an
earlier paper (Lemche 1937). The hypothesis*) of these
authors of a determinative "stream" spreading over the
under surface, around the anterior and posterior margins
and from them across the middle part of the upper sur-
face cannot explain these facts. This is still more strik-
ing in the case of a specimen of *Hyperdirphia tarquinia*
Cr. (Henke 1936 Taf. 12), in which the central field
on the upper side has narrowed so much as to cover
only a small area in the middle of the wing without
touching either the front or the hind margin.

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*) Still maintained by Kühn (1943).

In *Telea polyphemus* (Plate IV) the under side of the hind wing shows an interrupted central field, whereas that of the upper side is unbroken. This case, too, is not in conformity with the idea of a determinative stream springing from the under side and entering the upper side around the margins. If such a wing had arisen during Henke's experiments on *Philosamia cynthia* or Kühn & Engelhardt's on *Ephestia*, it would have led to the supposition that the determinative stream spreads in exactly the opposite direction, viz. from the upper to the under side.

On the under side of the hind wing in *Telea polyphemus* the foremost part of the field extends backward across the wing distally to the discoid spot, and the hindmost part extends forward along the proximal border of this spot. Thus, in this case two parts of the central field lie outside one another, showing that they cannot have been formed by the action of a true determinative stream spreading from a simple transverse axis. Such a case can only be explained by supposing that the stage in which the cells of the wing-surface attain their ability to react on the pattern-inducing impulses is not reached simultaneously in all places. The ability to react is first attained by the cells in the middle of the central field (in the "axis" of this field), and then, successively, by those lying axifugal to them, the whole process spreading like a wave to both sides (a "Determinationsvorgang" in the sense of Kühn & Engelhardt and Henke). If there is any local obstacle — as for instance the discoid spot — the ability to react of the neighbouring tissues may be impeded, as appears to be the case in *Telea polyphemus* mentioned above. Furthermore, it follows that this preparative process must take place independently on the upper and the under side of the wing, though it has probably in some very early stage started from a common source. The

shape of the transverse bands shows that the starting
point cannot be a true centre somewhere on the wing,
but that it must be regarded as having the shape of a
transverse "line" running across the wing (cf. Lemche
1937).

Köhler (1941) rejects this view by the words: "Da
diese Hypothese bisher durch keinerlei Tatsachen be-
legt ist und nach unsrer Auffassung eher einen Rück-
schritt bedeutet - - -". This standpoint, however, appears
to be due to a misunderstanding, which it seems neces-
sary to correct. The first suggestion of a view similar
to that held by me is to be found in a paper by Kühn
& Engelhardt (1933 p. 697), who say concerning the
determination of the transverse bands: "Mit der Aus-
breitung des Feldes tritt im Feldinnern in der Um-
gebung der Symmetrieachse an Stellen, die durch Struk-
tureigenthümlichkeiten des Flügels ausgezeichnet sind,
ein schwarze Schuppen determinierender Zustand auf".
Thus, these authors speak about special centres arranged
in a transverse row across the wing, the "Symmetrie-
achse", in spite of their hypothesis of a determinative
stream springing from the under side and reaching the
upper side around the margins of the wing. Hence I
would not regard it as a backward step if we were to
accept the idea of a first process determining the place
of the axis (that this process springs from the base of
the wing, as supposed by me (1937), has not been proved
and may perhaps be incorrect, but the existence of this
first step cannot very well be denied). Then, the second
step is the "Determinationsvorgang" or wave in the first
part of the pupal life which determines the amount of
spreading of the transverse band or bands across the
wing. This step has been investigated in detail by Kühn
& Engelhardt (1933) and others, and has been divided
into several different processes, the existence of which
I have no intention to doubt, nor have I had any reason

to discuss them in detail. Köhler (1941) incorrectly appears to be of the opinion that I would reject these results.

The decisive proof of a predetermination of the places from which the determinative wave spreads has, however, been given by Köhler (1932) himself, who has shown the wing in the prepupa to be folded in such a way that the folds indicate the normal places of the transverse bands which are finally developed in the late pupal life. These folds must of course have been arranged according to some determinative principles which act during the last larval instar or even before.

To sum up: all the authors appear to agree in regarding the axis of the transverse bands as determined before the labile period in the early pupal life. Furthermore, they agree in assuming the existence of an axis of symmetry running through some structurally distinct places ("präsumptive Musterörter") which are the first to respond to the impulses of the determinative wave of the transverse bands in the said labile period. In spite of this, Kühn and his collaborators maintain the hypothesis of a determinative wave springing from the under side of the wing. This hypothesis is at any rate just as unfounded on real facts as is my supposition that the first determinative step is caused by a process spreading in a distal direction from the wing base. Moreover — as mentioned above — some facts directly disprove Kühn & Engelhardt's hypothesis and consequently it must be abandoned. We must simply suppose that the processes which have been investigated in detail by these authors, spring from the axis of symmetry across the wing, on the upper side independently of the under side (which in *Ephestia* has no colour-pattern at all). In *Ephestia* the centres ("Musterörter") mentioned by these authors (and by Köhler 1941) are the spots where the longitudinal pattern on the veins intersects

that axis of the transverse bands. The prominence of these spots appears to be due only to the accumulative effect of these two independent pattern-inducing processes.

While in the examples discussed above the field of symmetry is narrowed along the "weak" veins, it is also possible to find wings which show just the opposite feature. Thus in *Crambus falcellus* (fig. 41) the distal band forms a very strong axifugal curve at the veins of the media and a smaller curve at cu_2 and a_1. This shows that weak veins are not simply less efficient than the other ones, but that all the different veins vary independently of each other in some degree when responding to the pattern-inducing impulses. This rule holds good for the intensity of the colouring as well as for the velocity of spreading of the impulses along the veins, and it may just as well be applied to the areas of the cells (the wing-ground) as to those covering the veins.

In some cases the influence of the longitudinal pattern is only small or nil, as is well illustrated in *Catagramma astarte* Cr. (Schwanwitsch 1930), where the distal and the proximal band (the "M_1" and "M_2" of Schwanwitsch) approach each other so closely as to fuse into a single, thin stripe. Normal specimens of the moth *Lygris testata* (fig. 39) have a broad band across the wing, just as other geometrids, but a single specimen shows a much narrower band (fig. 40). In the two cases mentioned the band appears to have contracted equally throughout its whole extent without any tendency to recede in the direction of the margins. In my opinion, these examples may be regarded as typical when the veins (or the longitudinal design) have lost their effect on the pattern. The tendencies of the bands to split into pieces and to form closed rings on the wings (Henke 1933) is probably due to the varying effect of the different veins.

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Thus, the part played by the veins — or in other words: by the longitudinal design — should not be forgotten in the study of the different transverse designs. The longitudinal design interferes in all parts of the wings with the transverse ones, and in many cases — e. g. in *Ephestia* — the "Systeme" in the sense of Kühn and his collaborators are not pure designs but composed of transverse and longitudinal components. Earlier authors have chiefly directed their attention towards the variation of these "Systeme", each of which is regarded as a physiological unity, within which the different elements follow one another in their variation. Gradually this view has been somewhat modified as the different elements turned out to show a certain independent variation (cf. Henke 1933 b, Clausen 1937), but at any rate as regards *Ephestia*, it has not hitherto been sufficiently emphasized that the different parts of the wing (the cells, and the areas covering the different veins) behave as separate unities, and similarly, that each cell and each single vein vary to some extent independently of the other ones, as is clearly illustrated by the aberrant vein cu_2.

To sum up: the pattern on the lepidopterous wings should be regarded as composed of two intersecting sets of designs, viz. the longitudinal one, and the other designs (the transverse symmetry-bands, the shadow, etc.) which run across the wing. One of these sets of designs may be lacking on a wing, but without giving equal consideration to both we cannot gain a full knowledge of the intricate problems of the wing-pattern.

9. Some genetic aspects of the distinction between transverse and longitudinal designs in *Ephestia kühniella*.

The distinction between different morphological components in the "systems" treated by Kühn and his col-

laborators as unities, makes a similar genetic difference probable, and actually the crossings made by Kühn & Henke appear to confirm such a supposition. These authors (1929) cross their strain V (formula given by Kühn & Henke: qqRRMM) with their strain XI (Formula QQrr--) and show the existence of a monohybrid difference in the appearance of the symmetry-bands, and another single-gene difference in the marginal spots. In 1932 they report crossings made between the same strain V and their strain IX (formula QuQumm), in which the difference in the symmetry-bands is likewise shown to be monohybrid. But although the authors mention a difference in the appearance of strains XI and IX, they do not define it in detail, and direct crossings between the two strains were not made on account of the early extinction of strain IX. However, the illustrations given by Kühn & Henke (strain V: Taf. II figs. 6 and 7, Taf. VIII fig. 1; strain IX: Taf. II figs. 11 and 12, Taf. VIII fig. 2; strain XI: Taf. II fig. 14) seem to show the cause of the difference. While strain V has a very faintly developed symmetry-system, strain IX shows a very strong blackening in the shape of long venous spots separated by a very light ground. Conversely, strain XI shows unbroken bands across the wing and only slight traces of the venous spots; the spots are at any rate not better developed than in strain V.

Thus we may suppose strain IX to possess a factor which influences the longitudinal design, and strain XI another one which gives rise to alterations in the symmetry-bands as such. This view receives some support if we examine the colour of the scales on the veins between the pattern-elements. Strains V and XI show no traces of black scales in these places, whereas in all the three figures given the veins of strain IX bear so many black scales that the course of the veins can be traced by means of them. Thus the longitudinal design

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is no doubt better developed in strain IX than in the two other strains.

Consequently, on calculating the coefficient of correlation between the symmetry-bands and the other pattern-"systems" on the wing — as done by Kühn & Henke — it is necessary to distinguish between the varition of the longitudinal design and that of the symmetry-bands proper, both designs being involved in the variation of the symmetry-"system" in the sense of the said authors. At the outset, the longitudinal design may be supposed to influence all the transverse "systems" in equal degree, while each of the impulses which really cause the transverse bands, etc. to develop may be of significance for a single system only.

Kühn & Henke (1929) show the marginal spots to be independent of the development of the ground of the symmetry-bands. However, it would be of much greater interest to investigate the possible interdependence of the marginal spots and the spots of these bands, i. e. the longitudinal design. Theoretically, an impulse of importance to the development of the longitudinal design may possibly also influence the spots placed along the blood-spaces, etc., along the outer margin of the wing. The gene R can hardly be identical with the gene Qu — which in that case would manifest itself in strain V by giving rise to well developed spots on the veins in the symmetry-bands — but the gene Qu may perhaps cause the marginal spots to broaden (and even partly to fuse). At least, from the illustrations of strain IX given by Kühn & Henke it would seem that the distances between the marginal spots are much shorter, and the individual spots less distinctly delimited, than in strain V.

As to the discoid spots, Kühn & Henke (1932) provide evidence that although in some cases there exists a certain positive correlation between these spots and

the symmetry-bands, it is by no means a rule, and the correlation may totally disappear. Accordingly there is little reason to suppose any influence of the longitudinal design on the development of the discoid spots.

As to the relation of the shadow to the symmetry-bands, the longitudinal design may be supposed to work on both of them in common, but the existing crossings cannot be used in a study of the correlation between these two "systems".

Summary.

1. The pattern on the wings of the Lepidoptera is shown to be formed to a large extent by interaction between a longitudinal design and some transverse designs (the symmetry-bands, the shadow, etc.).

2. The wing ground should be regarded as equalling the veins in its ability to react on the pattern-inducing impulses.

3. As regards their colour-pattern the margins of the wing behave as veins.

4. It is proposed to denote each pattern-element by a symbol of the transverse design (or part of design) combined with an index indicating the vein involved. Ground elements may be distinguished from those on the veins by a prefix. Such a procedure permits a comparison between the patterns of different Lepidoptera.

5. The pattern of *Ephestia kühniella* Zell. is shown to contain a much greater number of components than hitherto described.

6. The stem of the medial veins, and similarly the vein cu_2, both of which are generally regarded as rudimentary, are shown to have specific pattern-inducing properties and must be regarded as in no way rudimentary. They simply differ in structure from the other veins and influence the pattern in their own way; e. g.

the discoid design ("Discoidalzeichnung" of H e n k e & K r u s e 1941) is associated with the "weak" veins.

7. Each individual vein may differ in some property or other from the other ones, and the same is true of the wing-ground in the different cells between the veins.

8. K ü h n & E n g e l h a r d t (1933) and H e n k e (1933) advance a hypothesis of a determinative stream or wave springing from a centre on the under side of the wing and spreading to the upper side around the anterior and posterior margins, inducing finally the system of the symmetry-bands. This hypothesis is rejected, in so far as the wave is supposed to spring from an axis extending across the upper side of the wing independently of the under side.

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Explanation of plates.

The different pattern-elements are indicated by the letters symbolizing the system (in capitals) followed by those of the vein crossing it (cf. pp. 308—09). The prefix g indicates ground elements, the prefix v venous elements.

a_1 and a_2 anal veins. *am* anterior margin. *cu* (cu_{1a}, cu_{1b}, cu_2) cubital veins. *m* (m_1, m_2, m_3) medial veins. *pm* posterior margin. r_4 fourth radial vein. *sc* subcosta.

B basal spot. *D* (*DI*, *DII*) distal bands of the symmetry system. *P* (*PI*, *PII*) proximal bands of the symmetry system. *R* marginal spots. *S* shadow band. *W* root band.

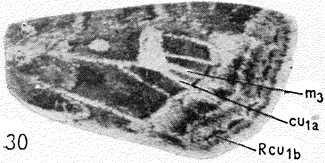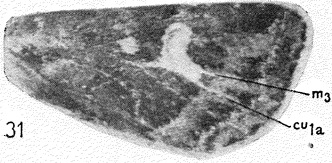All figures show the upper side of the left or right fore-wing of the imago (except fig. 32).

Pl. I

Pl. II

Pl. III

Pl. IV
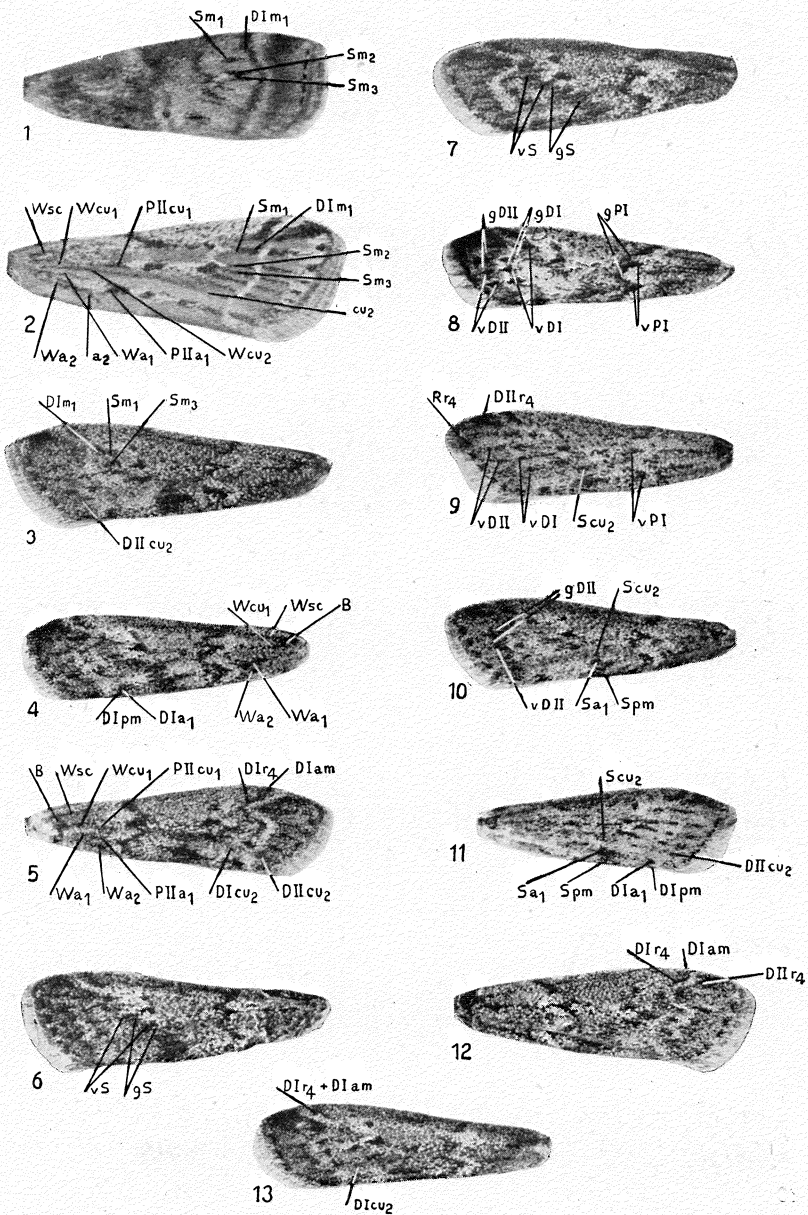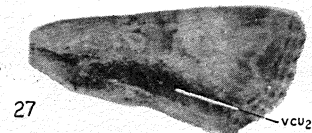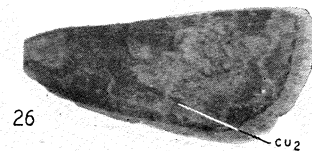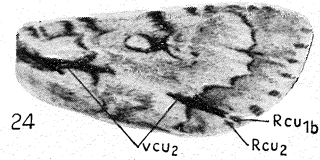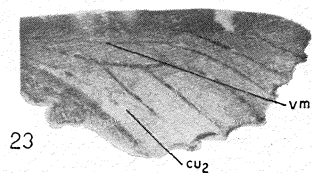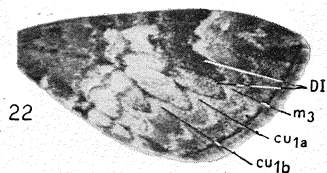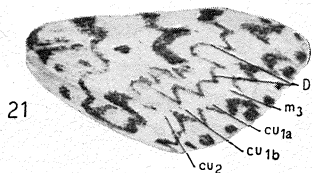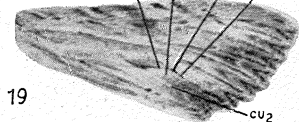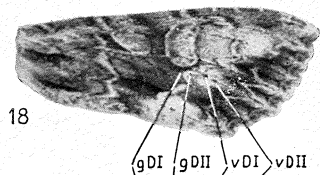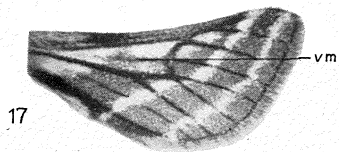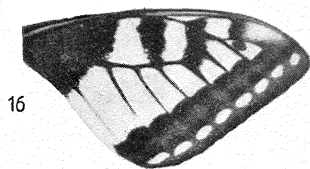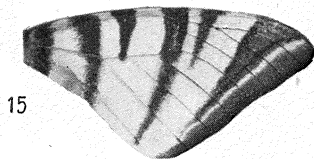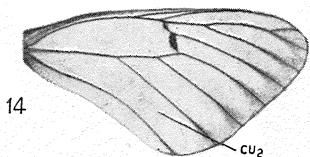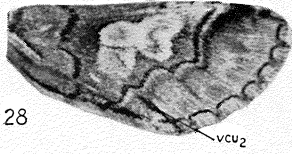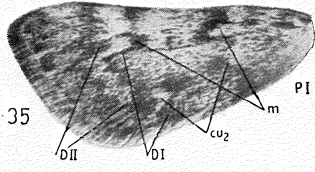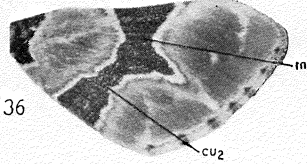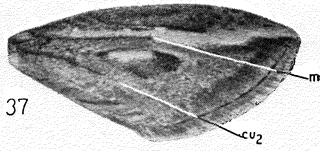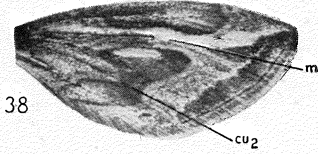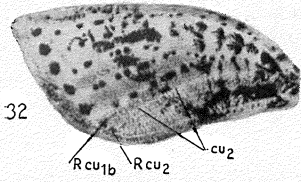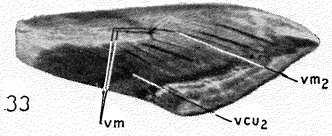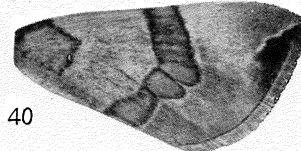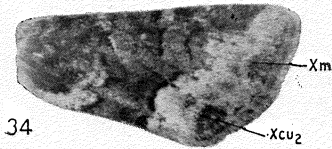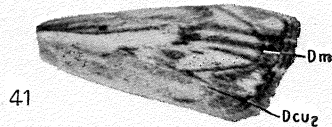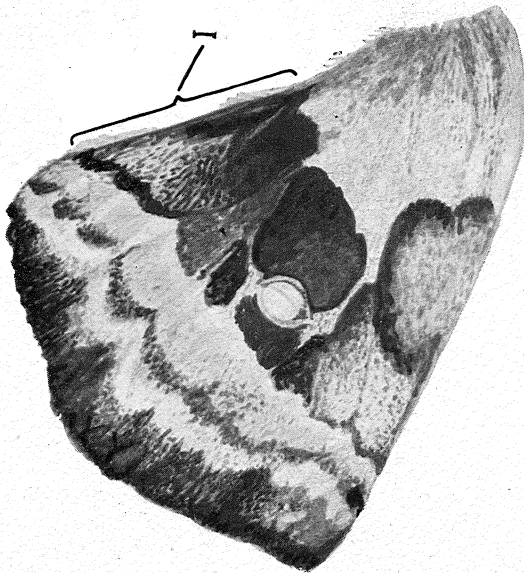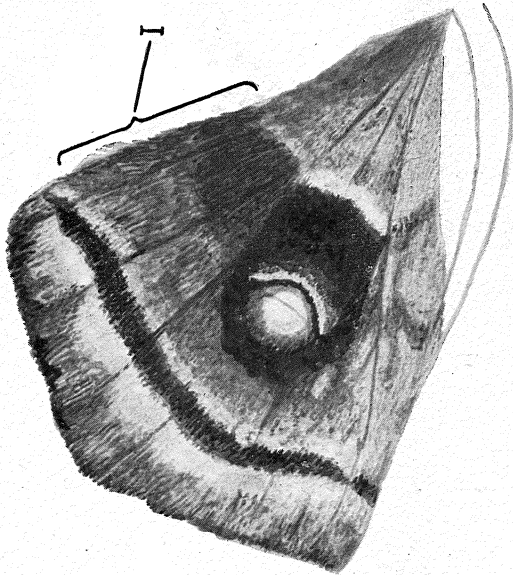
Plate I.

Fig. 1. *Phycita spissicella* F. × 3.5.
— 2. *Pempelia ornatella* Schiff. × 4.5.
— 3. *Ephestia kühniella* Z. (specimen 458 ♂ 55). × 3.
— 4. — — — (— 394 ♂ 35). × 3.
— 5. — — — (— 529 ♀ 23). × 3.
— 6. — — — (— 281 ♂ 8). × 3.
— 7. — — — (— 315 ♂ 72). × 3.
— 8. — — — (— 301 ♂ 54). × 3.
— 9. — — — (— 352 ♂ 58). × 3.
— 10. — — — (— 351 ♂ 3). × 3.
— 11. — — — (— 464 ♂ 24). × 3.
— 12. — — — (— 444 ♀ 32). × 3.
— 13. — — — (— 394 ♂ 43). × 3.

Plate II.

Fig. 14. *Aporia crataegi* L. × 1.2.
— 15. *Papilio podalirius* L. × 1.
— 16. *Papilio machaon* L. × 1.
— 17. *Biston zonarius* Schiff. × 3.
— 18. *Hadena monoglypha* Hufn. × 2.
— 19. *Hadena lithoxylea* Fabr. × 2.
— 20. *Codonia annulata* Schultze. × 2.7.
— 21. *Lymantria monacha* L. × 1.5.
— 22. *Cidaria truncata* Hufn. × 2.5.
— 23. *Odontosia carmelita* Esp. × 2.
— 24. *Acronycta psi* L. × 2.
— 25. *Acronycta alni* L. × 2.2.
— 26. *Miana bicoloria* Vill. × 3.5.
— 27. — — — × 3.5.

Plate III.

Fig. 28. *Diloba coeruleocephala* L. × 2.2.
— 29. *Taeniocampa munda* Esp. × 2.2.
— 30. *Luperina haworthii* Curt. × 3.5.
— 31. — — — × 3.5.
— 32. *Pieris brassicae* L. (pupal wing). × 3.5.
— 33. *Sphinx ligustri* L. × 0.7.
— 34. *Hadena strigilis* Cl. × 2.7.
— 35. *Aglossa pinguinalis* L. × 2.7.
— 36. *Ortholitha sagittata* Fabr. × 2.7.
— 37. *Chesias legatella* Schiff. × 2.2.
— 38. — — — × 2.2.

Fig. 39. *Lygris testata* L. × 2.5.
 — 40. — — — × 2.5.
 — 41. *Crambus falsellus* Schiff. × 3.5.

Plate IV.

Telea polyphemus Cr. Upper (left) and under (right) side of the
hind wing showing interruption of the central field on the under
side. *I* the central field and its dark borders. (After Henke 1936,
redrawn).

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