

broken-line curve in fig. 6 the correction indicated by the full-line curve. At the starting point and the end the correction is zero. At the highest point with an ordinate  $a$  we get a correction:

$$a(5 + 5) : 2 \times 200 = \frac{1}{40} a, \text{ or } 2.5\%$$

of the maximum ordinate.

In my experiments I used a condenser of 2 mikrofarad,  $R$  and  $r$  being  $10^6$  Ohm each. The oscillographic record was made with a stringgalvanometer. Fig. 7 gives an example of the curves obtained in this way.

**Zoology.** — "*The wing-design of mimetic butterflies*". By Prof. J. F. VAN BEMMELEN.

(Communicated at the meeting of Nov. 27, 1920).

In a paper: On the phylogenetic significance of the wing-markings of Rhopalocera, read before the meeting of the second International Entomological Congress at Oxford in 1912, I made the casual remark that "while inspecting the series of butterflies in search for specimens showing the primitive colour-pattern, I was greatly impressed by the considerable percentage of mimetic forms among my harvest. So the idea occurred to me that perhaps Mimetism might, at least to a certain degree and for a limited number of cases, be explained by supposing the resemblance between two or more non-related forms to have started at an early period, when the ancestral types of different butterfly-families looked more like each other than nowadays, on account of the primitive colour-pattern common to them all".

Since those days I have tried to clear and widen my ideas about the real character of the primitive colour-pattern, especially by a detailed analysis of the wing-design in original forms such as the Hepialids, and by its comparison to the pattern of the body. These investigations have led me to a modified conception of primitiveness in pattern: the occurrence of sets of uniform spots, regularly arranged in rows between the wing-veins, and spread over the entire wing-surface, appearing to me as a still more original condition than the concentration of the markings in the shape of a stripe along the middle-line of the internervural cells. But this does not in the least weaken my conviction, that this latter arrangement has retained a considerable amount of primitiveness also, and that its origin lies far beyond the beginnings of genera, families, nay of the whole order of Lepidoptera.

Since then the Groningen Zoological Laboratory has acquired the magnificent collection of Lepidoptera left by the lamented MAX FÜRBRINGER in Heidelberg. Thereby I was enabled to study actual specimens of mimetic butterflies in nature and this made me wish to return to the question of Mimetism in general, but then considered exclusively from a purely morphological standpoint. I desire therefore to avoid carefully the biological side of the question, though I may be allowed to express my conviction that the often

striking superficial similarity between forms belonging to widely different groups, can hardly fail to provide certain advantages in the struggle for existence either to one or to both of them, or at least must have done so in former periods of their occurrence on earth.

I shall henceforth restrict myself to a careful comparative analysis of the colour-pattern. But before entering on this task, I wish to remark that the phenomenon of mimetic resemblance can never be ascribed to the influence of a general law, and consequently the different cases of Mimicry must be judged separately, quite independently of each other. That e. g. a *Sesia* resembles a wasp, cannot possibly stand in any genetic connection to the mimetic similarity between a *Dismorphia* and an *Ithomiid* or a *Heliconid*, or between a set of species of the latter families amongst each other. Nor can this occurrence of wasp-like *Sphingids* stand in any relation to the existence of other members of that same group, which seem to have assumed the habitus of humble-bees.

Mimetic resemblances consequently must be considered as of casual origin, and the considerable number of conditions, which had to be fulfilled before a real case of Mimicry could enter into existence, make us readily understand the relative rareness of the phenomenon, and its apparently capricious distribution over the animal kingdom (as REBEL has so judiciously pointed out).

Though, as mentioned before, I am inclined to acknowledge the high probability, that in many cases the close superficial and simulating resemblance existing between mimic and model is extremely useful either to the mimic only or to all the members of the mimetic set, I am also convinced that no impartial judgment can possibly be formed without carefully abstaining from all considerations about this hypothetical and problematic usefulness, and exclusively regarding the mimetic forms from a purely morphological standpoint, that is to say investigating them according to the very same principles and rules that have proved useful for the understanding of the colour-pattern of insects in general, and the laws that we could deduce from this study. To this conclusion we are logically led by the observation, that mimetic patterns do not differ in any special feature from colour-designs in general, but on the contrary agree with the non-mimetic patterns, at least when these are embraced in a general view. Solely when we compare the mimetic forms with their nearest allies: the non-mimetic members of the same genera, do we meet with certain cases where they seem to depart widely from the common generic type, though even this by no means can be called the general rule. By the adherents of the Mimicry-hypothesis this

apparent diversion from the original pattern is attributed to the influence of natural selection, leading gradually to a perfect though wholly superficial and spurious similarity with the model.

In order to be able to accept this hypothesis, it is obvious that we are obliged first to prove the assumed deviation from the primitive common type of the genus or family. We ought to abstain from accepting it a priori as a fixed truth, but should try to reconstruct the original common genus- or family-type of colour-design by a perfectly impartial comparative investigation of all the existing members of the group, mimetic as well as non-mimetic, judging them exclusively after the features of their markings, without the least regard to any biological profit these markings might possibly procure them.

The value of these considerations can best be appreciated by their application to a few concrete examples.

In the famous paper of BATES on the resemblance between members of the Pierid genus *Dismorphia* (*Leptalis*) and certain South-American *Ithomiids* and *Heliconids*, the author figures a perfectly white species of the said genus, side by side with the mimetic forms, and expressly states that this represents the original type of that family. It necessarily follows that he considers the mimetics as widely deviated from this type. PUNNETT, in the chapter on "Mimicry Batesian and Müllerian" of his valuable critical review "Mimicry in Butterflies", expressly puts forward that this is the current view among the supporters of the mimicry-theory, where he says: "We come back to our Pierine, which must be assumed to show the general characters and coloration of the family of whites to which they belong" . . . . and "If however they could exchange their normal dress for one resembling that of the *Ithomiines*". (The italics are mine).

Doubtless BATES did not for a moment presume that the case might as well be exactly the reverse: the mimetics representing the more original, least altered forms, while the whites, under the prevailing influence of albinism, have considerably departed from the primitive condition.

To make a choice between these two opposite views, we must in the first place undertake a careful and complete investigation of the various colour-patterns of all the members of the genus *Dismorphia* and different other genera of Pierids, and after that come to a clear understanding about the real nature of the differences between the mimetic and non-mimetic forms.

These differences can be summarized under three heads: those of pattern, of hue and of shape.

Beginning with the first, we may start with the assertion, that a really objective analysis of colour-patterns necessarily involves the exact consideration of the whole complex of markings in all its details. So we must as well pay attention to the underside as to the upper surface, and attribute the same importance to those features, in which the mimics differ from their models as to those in which they agree with them. Viewed from this standpoint (which up till now has very rarely been observed), we easily come to the conclusion, that all the elements, which enter in the composition of the pattern of mimetic forms, can be traced back to those of their non-mimetic congeners, and therefore may be counted among the characteristic features of the genus (or family) to which the mimics belong.

The same remark holds good for the particular hues the mimics display, and even for the apparently aberrant shapes they sometimes assume. When e. g. the mimetic *Dismorphia*'s differ from the majority of the species belonging to the genus by the greater length and the more slender contour of their wings and body, the question if such a form of butterfly might really be regarded as aberrant, has carefully to be considered, instead of being accepted as solved. That it deviates from the "common" type, is obvious, but since when has mere commonness been regarded as a proof of primitivity? Do the Monotremes represent a widely aberrant and deeply modified type of Mammals, merely because they are (at present) restricted to two families? The broad square shape of the majority of Rhopalocera, with their rounded hind- and triangular forewings, including a short body, may far more probably be itself a modification of the narrow-winged form with slender body, such as we find in so many Sphingids and Heterocera, especially in an eminently primitive family as the Hepialids. Even among Rhopalocera themselves this latter habitus is no rare exception, for we find it prevailing in several families, e.g. the Ithomiids and Heliconids. So in matter of shape the resemblance between these "models" and their Dismorphian mimics can safely be attributed to their both having remained faithful to the more ancient form of Lepidopterous insects. Its antiquity may even reach far over the limits of this order, for the same contours prevail among many other, less specialised groups of insects, e.g. Odonata, Neuroptera or Trichoptera. Coming once more to the question of colours, it is easily conceivable that white need not at all be regarded as the most primitive hue in the Pierid family, several other colours: red, yellow, brown, black, occurring just as frequently, especially on the under-

side of the wings. Only its prevailing tendency to spread over large parts of the wing-surface and obliterate the original pattern by albinistic discoloration, gives to the white hue such a prominent place in the colour-scale of this family. But the same role is played by all the remaining shades in different cases. In this regard it deserves our attention that DIXEY, the eminent Pierid-specialist, in his paper on the phylogeny of their colour-pattern, does not start from a uniformly white groundform, but from a dark-hued regularly spotted type as *Eucheira socialis*.

Out of the numerous instances of Mimicry the astonishing case of *Papilio dardanus* "with his harem of different consorts, all tailless, all unlike (the male) himself, and often wonderfully similar to unpalatable forms found in the same localities" (PUNNETT), seems to me especially fit to test the validity of my views. As PUNNETT states: "From (a) long series of facts it is concluded that the male of *P. dardanus* represents the original form of both sexes".

According to my standpoint the only "facts" on which such a conclusion should be based, are features relating to the colour-pattern of the male and that of the different females, compared to each other and to those of their fellow Papilionids. But the above-mentioned "facts" are of an entirely different and wholly inadequate character, for they are connected with the mimetic resemblance of the females to Danaid models, and their apparent divergence from the bulk of Papilionids.

An impartial scrutiny of the relation in pattern between the male form and the manifold females should be undertaken entirely regardless of any such resemblances. When conscientiously remaining true to this principle, and exclusively applying the general rules for the consideration of the colour-pattern, we are forced to the conclusion, that the male form, instead of being the original, is by far the most-modified.

The opposite opinion seems chiefly to have root in the unconscious susceptibility of the human mind to first impressions. We are so accustomed to associate the type of a Papilionid butterfly with the swallow-tail-image, that we involuntarily consider those members of the family, which by their tails, their characteristic markings at the inner angle of the hind-wings, their yellow and black hues, come nearest to this apparent ground-form, as the original representatives of the family. But when we cast a general look over the whole of it, we encounter numbers of species in which the tails are absent, either in both sexes or in one of them, and in the latter case it need not exclusively be the female sex, which lacks tails: *P. memnon*.

for instance showing the opposite case. It should also be taken into account, that in closely-related groups, e.g. the *Ornithoptera*, *Anti-machus* and *Druryia*, which for good reasons are considered highly primitive in many features, there is not the slightest indication of tails. And as to the original groundform of *Rhopalocera* in general, this can scarcely be supposed to have carried such prominent appendages at its hind-wings.

Though all males of *P. dardanus*, together with some of its (non-mimetic) female forms, can be considered as corresponding to only one type, this type undoubtedly is subject to very wide variation, and the trend of this variability lies in the direction of the pattern of the mimetic females. So we might consider those males which in the extension and the design of their markings come nearest to the females as the least-altered ones, and this view is found to coincide with the general assumption, that absence or restriction of markings is a consequence of their obliteration by the transgression of hues from their original centre over neighbouring areas.

In the male of *P. dardanus* it is the yellow shade which gets the supremacy, and more or less reduces the black markings to total extinction. Consequently racial forms in which the black shows a greater extension, like *meriones*, *tibullus* and *trimeni*, represent the less modified forms of the male type. Comparing these variations with the mimetic females, we see that they agree with them to a higher degree than the more-uniformly yellow males, and that the special features in which this nearer agreement shows itself, are in fact precisely those details of pattern, wherein these females seem to deviate from the assumed specific *Dardanus*-type, and to simulate their Danaid models.

Let us consider e.g. the narrow black border along the front-margin of the forewing of the male butterfly and those female forms, which bear the masculine type. Some specimens of the typical *Dardanus* show a rather imperceptible thickening in the middle of this rim, proximad to the discoidal nervure. In *tibullus* this thickening is much more striking, in *meriones* and *antinorii* it can touch the back-limit of the discoidal cell, and in *trimeni* it stretches as a black crossbar in an outward and backward direction up to the dark marginal area along the outer wingborder, thereby cutting up the yellow area into an antero-external and a postero-internal part. E. HAASE: Untersuchungen über die Mimicry auf Grundlage eines natürlichen Systems der Papilioniden (Bibl. Zool. III, 1893) in his Fig. 4 on page 13, numbers this bar as N°. IV + V. Comparison with the female forms *cenea*, *acene*, *niavina*, *ruspinae*, *trophonius*, *trophonissa*, *hippocoon*,

*hippocoonides*, clearly proves that in all of them this same oblique dark crossbar is equally present, but that in its distal part, outside the discoidal cell, it becomes broadened by junction with the nearest distal dark marking along the discoidal nervure (HAASE's Terminal-band). In consequence of this junction the bar occupies the proximal part of four successive internervural cells (R., M<sub>1</sub>, M<sub>2</sub>, M<sub>3</sub>: HAASE'S VR 1 + 2 + 3 + 4).

By the occurrence of this crossbar the light-hued middle area of the forewing is divided into a smaller apical blotch and a larger more or less triangular field along the hinder (inner) margin, the latter passing without interruption into the light area which fills the proximal part of the hindwing. This division is one of the prominent features on which the similarity with Danaids depends. But it would be quite inadequate to ascribe the occurrence of this bar to secondary deviation from the original specific type under the influence of natural selection in connection with Protective Mimicry. For the same bar occurs in the females of a considerable number of nearly allied species, e.g. *cynorta*, *homeyeri*, *jacksoni*, *ucalegon*, *auriger*, *adamastor*, *agamedes*, whose males, at least part of them, show an uninterrupted chain of light-hued internervural spots, which increase in size from before backward, and on the hindwing blend to the light middle-field. These spots are separated from each other by longitudinal dark striae, caused by the more or less pigmented wing-veins. The anterior light spot in the apical field of the forewing of *P. dardanus* is the first of the series, it occupies the interspace between the roots of nervus radialis 4 and 5 (radial fork) and we get the impression that this position has something to do with its more marked persistence, by means of which it remains visible, when the other spots are effaced either by light or by dark colour-overspreading. Yet this apical spot also is not exempt from reduction or obliteration: in some specimens of all forms of *dardanus*, male as well as female, it may be reduced to a mere speck, or be wholly absent (comp. the figure of the *trophonius*-female on PUNNETT'S Pl. VIII).

Nor is the above-named dark cross-bar restricted to *dardanus* and its nearest relatives, it occurs as well in a number of other Papilionids, e.g. *hesperus*, *pelodurus*, and others.

In numerous other cases the tendency towards the formation of the cross-bar is equally present, but does not lead to such a conspicuous partition between an anterior and a posterior light area. In *epiphorbas* e.g. the forewing is almost entirely black, with the exception of a hooked central green part. The foremost leg of this

hook is formed by the light blotch separating the terminal bar from the third discoidal one, the hindmost leg by three remnants of the above-mentioned chain of light areas in the internervural cells.

Traces of the bar can also be remarked in *theorine*, *latreillanus*, *ausorü*, *phoreas*, *oribazus*, *charopus*, which means, that a tendency towards interruption of the chain of light blotches is manifest in numerous and very different members of the Papilionid tribe. Nor is this tendency restricted to the forms with tripartite wing-design, it occurs as well in richly spotted forms e.g. *cyrnus*, *demodocus*, *rev*, *mimeticus*, *ridleyanus* and even in regularly checked ones as *anti-machus*. In the majority of these last-named butterflies the tendency towards interruption of the light chain only shows itself in a reduction of one or two members of this chain to specks, one in *anti-machus* and *mimeticus*, two in *rev*.

Applying the above considerations to other details of the pattern, we are always led to the same conclusion. Especially convincing is the careful analysis of the pattern on the underside of the different *dardanus*-forms, and its comparison with that of the upperside. It shows us, that the median dark striae in the internervural cells have much better maintained themselves on the underside, but that their remnants can be more or less retraced on the superior surface, especially on that of the hindwings. Consequently such a condition of this pattern, as is seen on both sides of the hindwings of the *hippocoön*- or *trophonissa*-form, where these striae are sharp and run without interruption through all the cells (thereby agreeing with *zalmoxis* and similar forms) may, as I said before, be considered as primitive. In regard to these striae two remarks may be offered. The first refers to the pattern of the upperside of the male hindwing, on which the submarginal bar presents all degrees of variation, from a broad complete, uninterrupted belt to a few widely separated irregular black markings. In the latter cases the reduction has either led to the persistence of three blotches: an anterior (exterior), middle and posterior (internal) one, or has only left the two extremes. When the middle one is still present, this very often assumes the character of an internervural stria, and thereby betrays its allegiance to the markings on the underside.

The second remark refers to the colour-pattern of a near relative of *dardanus*, viz. *P. cynorta* (alleged forms included, as *norcyta*, *jacksoni*, *fullehorni*, *echerioides*, *cypraeofila* etc.). Here also a similar striking difference exists between male and female, though the latter occurs only in a single form, which shows a mimetic resemblance to *Planema epaea*. The similarity chiefly depends on the presence

of the before-mentioned oblique dark cross-bar in the forepart of the forewing, and on the series of black median striae in the internervural cells of the hindwing. The male differs from the female by the absence of the cross-bar; the medial area of the forewing thereby showing the uninterrupted chain of internervural light spaces, which diminish in size towards the apex. In contrast with *dardanus*, the root-part of the hindwings in *cynorta* is dark, which causes a closer junction between the central chain of light markings on the fore- and on the hindwings. When comparing these dark root-fields with their counter-parts on the underside, they are seen to be present also there, but tinged in a bright orange-brown hue, intersected by a system of darker lines which mark the wing-veins and the internervural striae. As these lines reappear in the distal part of the wing, it is evident that they are interrupted in the middle-area by the white discoloration. So we are justified in assuming that in more original forms both the veins and the striae will run uninterruptedly over the whole surface of the hindwings (on upper- as well as on underside) and we find the affirmation of this assumption in a great many forms of butterflies, belonging to different groups, and counting among them models as well as mimics (e.g. *Planema tellus* and *Pseudacraea terra*, see PUNNETT, Plate IV, Fig. 3 and 8). In the *nireus* and *oribazus*-groups e.g. the upper surface shows a tripartite colour-pattern with light (azure) middle-bar, and black inner and outer region, but only the slightest traces of nervural and internervural striae, while these latter are distinctly marked and in complete array on the underside of many of the appertaining forms (e.g. *nireus*).

When therefore it can be proved for every single detail in the pattern of mimetic forms that it belongs to the stock of generic, familiar or ordinal hereditary features by which the outward appearance of the several members of a group is effected, there is no reason left for ascribing the total effect of the combination of all these details to the influence of Protective Mimicry. Nor can the phenomenon of Polygynomorphism itself be attributed to this cause, it has to be considered as a peculiar complication of sexual difference in general, occurring in certain groups of butterflies, as e.g. Papilionids. That some of the polymorphic females may profit by their accidental likeness to unpalatable forms, is indeed very probable, but this profit can merely be a consequence of the casual similarity, never its cause.

The phenomenon of Polygynomorphism itself should be classed with other cases of Polymorphism, either in connection with sexuality or independent of it, as seasonal, geographical, racial plurality of

type. In the end, it is of the same nature as specific differentiation in general.

So in *Hepialus humuli* the white masculine form has evidently lost the primitive specific livery, which is still preserved by the female and by the Shetland-male.

Though in general my opinions on these subjects disagree with those of HAASE, I feel much satisfaction in making the following quotation from the concluding passage of his "Resumption" (p. 112): "The mimetic transformation was preceded in most cases by atavistic phenomena from the side of the females, which in the beginning reached back to the patterns of the nearest relatives, but as the process proceeded, passed over to those of more distanced forerunners and in this way procured the material for the mimetic adaptation".

So HAASE attributes the uniforms of mimetic females to hereditary influences, instead of considering them as the consequence of secondary deviations from the primitive specific type.

Groningen, Nov. 1920.

**Physics.** "On the Equation of State for Arbitrary Temperatures and Volumes. Analogy with Planck's Formula." II. By Dr. J. J. VAN LAAR. (Communicated by Prof. H. A. LORENTZ).

(Communicated at the meeting of November 27, 1920).

### § 7. Some Notes to § 1—6.

It will be soon two years ago that I wrote the first part of this Article<sup>1)</sup>; studies of various kinds prevented me from continuing the subject, and not until now could I take it up again.

Before I proceed to the derivation of the equation of state, based on the found general expression (6) on p. 1194 loc. cit. for the time-average of the square of velocity  $u_t^2$ , expressed in  $u_0^2$  (in which  $u_0$  represents the velocity with which the considered molecule passes the neutral point in its motion to and fro between two neighbouring molecules), I will add a few remarks to elucidate and complete what was treated before.

1. In the first place a few words about the transition of some "linear" quantities to the corresponding "spatial" quantities.

If we have linear quantities, we can consider all our velocities as the components of the relative velocities directed normally; as we always imagine a molecule moving rectilinearly to and fro between two molecules at rest. We know that  $\overline{u_r^2} = 2\overline{u^2}$ , and that the mean value of the component of  $\overline{u_r^2}$ , directed normally, in its turn is the third part of this, so that we have (cf. also p. 1195 loc. cit.):

$$\overline{(u^2)_n} = \frac{2}{3} \overline{u^2}.$$

Hence we may write:

$$\frac{1}{2} Nm \overline{(u_r^2)_n} = \frac{2}{3} \times \frac{1}{2} Nm \overline{u^2},$$

or also, denoting the time-average by the index  $t$ :

$$\frac{1}{2} Nm \{ \overline{(u_r^2)_n} \}_t = \frac{2}{3} \times \frac{1}{2} Nm \overline{(u^2)_t}.$$

In this  $\frac{1}{2} Nm \overline{(u^2)_t} (= \frac{1}{2} pv \text{ in ideal gases}) = \frac{1}{2} RT$ , so that we may henceforth write:

<sup>1)</sup> These Proc., Vol. XXI, p. 1184.