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Zoology. — "*The wing-markings of Arctiidae*". By Prof. J. F. VAN BEMMELEN.

(Communicated in the meeting of November 24, 1917)

As exposed in former publications, based on my investigations of Rhopalocera and Hepialids, the analysis of wing-markings leads to the assumption of an original pattern, common to all members of the group, and modified in various but not independent ways in the several families, genera, and species. At the same time these studies have induced me to propose a set of general rules about wing-design: among others the original identity in the markings of fore- and hindwing, upper- and underside, etc., these conclusions in many cases agreeing with those of my predecessors, notably with EIMER's.

Therefore I felt a little astonished when I found that DE MEYERE, in his recent publication: Zur Zeichnung des Insekten- im besonderen des Dipteren- und Lepidopterenflugels, though continually referring to my investigations, and paying them the honour of his critical remarks, only superficially mentions the above named hypothesis about a general primitive pattern, and also pays but slight regard to the necessity I insisted upon, of comparing in every case the two wing-pairs as to both their surfaces and of always asking where the original conditions have remained most plainly. In some passages DE MEYERE cursorily pays attention to differences between upper- and underside, fore- and hindwing, but in many others he does not even mention which part of the wing-design he has in view, nor does he seem inclined to deduce general rules from the rich treasure of his observations, except his assertion that: "also here (viz. amongst Lepidoptera) "though on a more restricted scale" (than amongst Diptera) "the various directions of the development of wing-markings play a part, the stress being laid by him on the word "various". Yet, according to my view, the detailed study of the underside of *all* Lepidopteran-wings, and its comparison with the upper surface, is all the more necessary, because especially in Heterocera the inferior wing-side has practically been disregarded, as is proved by the almost complete absence of figures, even in the most recent works. I therefore prepared for several years an attempt to supply this deficiency, and had come to the conclusion,

that the above mentioned general supposition, as well as the rules about colour-design connected with it, may be applied to all groups of Lepidoptera; the undersides of Heterocera-wings showing a far greater fundamental similarity in design than could possibly be concluded from the far more altered condition of the upper surface, where the contrast between fore- and hindwing is usually very sharp.

Evidently the detailed comparison of all existing Lepidoptera-patterns must be claimed as a condition for such a general inference, but at the same time it may be asserted, that its probability increases with every new group, for which its applicability can be proved. On this account I consider the special inspection of small and sharply-limited families highly important, and think this should precede a general survey of the whole order, as given by DE MEYERE, in which necessarily each family can be examined only cursorily and superficially.

That I have chosen Arctiïdae this time, is to a certain point a matter of accidental predilection, Sphingidae or Noctuïdae being probably as suitable as a starting point, Geometridae even more so.

Partly my choice may be justified by the vivid colours and the seemingly fantastic markings which characterise many members of this family and by which probably also DE MEYERE has been moved to mention the Arctiïdae in the very beginning of his paragraph on Lepidoptera as an uncommonly clear and complete instance of the dispersal of spots, in connection with the system of longitudinal wingveins, and frequently to choose his examples from this family in the course of his treatise.

Arctia caja may serve as a fit starting point, especially so because on the superior wingsurface of this form the contrast between fore- and hindwing is particularly strong, in regard as well to the pattern as to the hues, displayed in its composition. The forewing shows an apparently bizarre marmoration in creamy white and darkbrown, the hind one a group of five black blotches, with a lustrous blue centre and a thin yellow outer circle, arranged on a background of crimson.

This same contrast in pattern and hues between fore- and hindwings may be retraced in several congeneric species, but with many modifications, which in my opinion are very instructive. Though I do not propose in this paper to consider the colours as such, I wish to remark, that red is often replaced by yellow, brown by black. The creamy white may rise to deep yellow, the blue lustre on the black markings of the hindwings may be absent, as also their yellow lining. Lastly, the contrast between light and dark hues may almost

or completely disappear, fore- and hindwing or one of them becoming selfcoloured.

The comparison of the upper side of the forewings in different specimens of *Arctia caja* already leads to the conviction, that the capricious winding of the white interspaces between the dark-brown areas may be deduced from a regular alternation of light and dark transversal bars. For along the anterior margin this regularity is unmistakably present in all specimens, as well as in the majority of the remaining Arctiïdae and in cognate families, seven dark blotches alternating with six light spaces, if we count from the wingtip to the root, the latter being frequently covered by a narrow white tegulum. Indicating the dark spaces with the cyphers 1 to 7, the light bars with the letters A to F, we observe that A, B, E and F communicate with a longitudinal white streak, which winds along the median part of the wingflat from the root till near the outer margin, and sends out four transverse branches to the back-margin. The question arises, whether these branches may be considered as the prolongations of a corresponding number out of the 5 anterior transverse bars, and if so, of which of them; I prefer, however, to leave this question unsolved for the present. The white bars C and D on the contrary are isolated spots; D reaching to the radial nerve, C advancing somewhat farther towards the middle, and so entering the discoidal cell.

The light bars are not all of the same width, but they generally are somewhat narrower than the intervening dark spaces; yet in different specimens the dimensions are highly variable.

This variability has been studied and statistically arranged for a very extensive material by K. SMOLIAN[1]). As however his investigations do not in the first place touch on the phylogeny of the colour-pattern, they need not be considered here further. I only wish to remark, that SMOLIAN also assumed seven dark and six light transverse bars on the forewings, and found them back on the hindwings. Of this set of six lightcoloured bars on the forewings a certain number, varying from nought to six, might reach the hindmargin. A look however at the fourteen schematic figures, by which SMOLIAN represents these seven cases with their various sub-forms, shows that in none of them except the very last one (all six light bands extending across the whole wing) the fourth light spot (counted from the wing-root), proceeds farther than the hind-limit of the

[1]) Kurt SMOLIAN, Ueber die Variabilität des braunen Bärenspinners und die Beziehungen desselben zu den ihm nächstverwandten Arten, Jenaische Zeitschr. f. Nat. Wiss. Vol. L, 1913.

discoïdal space, this same fourteenth variation moreover not presenting a pure instance of real continuity of the bars from fore- to

Fig. 1. Arctia caja.
Schematic wingpattern after SMOLIAN.

hindmargin, but only a case of partial self-colour, which has caused the almost complete disappearance of dark bars in the proximal wing-area with the exception of a single isolated little spot, this part of the wing therefore having changed almost entirely to an uninterrupted light field.

One might feel inclined to conclude from this observation that spot 4 (SMOLIAN's *d*) differs in character from the rest of the six spots along the front-margin. I doubt however the soundness of this conclusion, on account of a comparison with allied species, in which this spot, though restricted in the majority of them to the area of the discoïdal cell, yet sometimes shows distinct connections with a light bar extending to the hind margin, e. g. *Arctia hebe* and *fasciata*. In a still stronger degree this is the case in *Pericallia picta* (Seitz, Grosschmetterlinge Vol. X, Taf. 24) and *Carminopyga lichenigera* and *proserpina* (ibid. Vol. II, T. 17, *g* and *h*), which show six dark

and six light bars running from fore- to hindmargin in unvarying width. At the same time it may be observed that the six dark bars of *proserpina* correspond to the seven brown areas of *caja*, and that the condition in *lichenigera*, where seven light and seven dark bars occur (those near the outer margin being incomplete) leads to the supposition that in *proserpina* and *caja* the most proximal light bar, i. e. the one near the wing-root is absent.

Let us apply to the study of the pattern on the upper side of the forewings in *Arctia caja* the usual methods of investigation, scil.:

1. Comparison of the condition of the colour-markings in different specimens, especially in varieties and aberrations.
2. Comparison with the pattern of the underside.
3. „ „ „ „ on upper- and underside of the hindwing.
4. „ „ „ „ of other Arctiids.
5. „ „ „ „ of allied families.

These all of them lead to the same conclusion SMOLIAN came to, scil: that the basis of this pattern are seven transverse dark bars, but at the same time clear indications are seen, that these bars owe their origin to the coalescence of spots, instead of having secondarily dissolved into series of spots, as was SMOLIAN's view.

Equally convincing are the proofs that originally the patterns on fore- and hindwings, as well as on upper- and underside, were identical; the strong contrast in this regard existing between the two wingpairs, especially at the superior surface, therefore being a consequence of secondary modification. In the same way the study of the underside clearly proves, that although the original similarity, both in pattern and in hues, between fore- and hindwing, has better maintained itself than on the upper surface, yet its colour-markings have suffered a reduction, which in many cases has only left the discoïdal spot, sometimes accompanied by a few markings at the front- and outer margins. With respect to this existence of special wing-areas, in which the darker pigment accumulates by preference, and maintains itself to the very last, the Arctiïds behave in correspondence to general rules, which can be laid down for all Heterocera, may be even for all Lepidoptera and other winged Insect-classes.

According to my view the arguments, leading to the above named conclusion, can only be discussed with the aid of numerous coloured illustrations and detailed descriptions, but this seems to me rather unnecessary, it being sufficient to point to such forms as *Rhyparia purpurata*, in which the upper surface of the forewings has preserved

the original rows of spots in almost complete and regular state, except the second from the inner side. (Fig. 2 and 3).

Underside Upperside

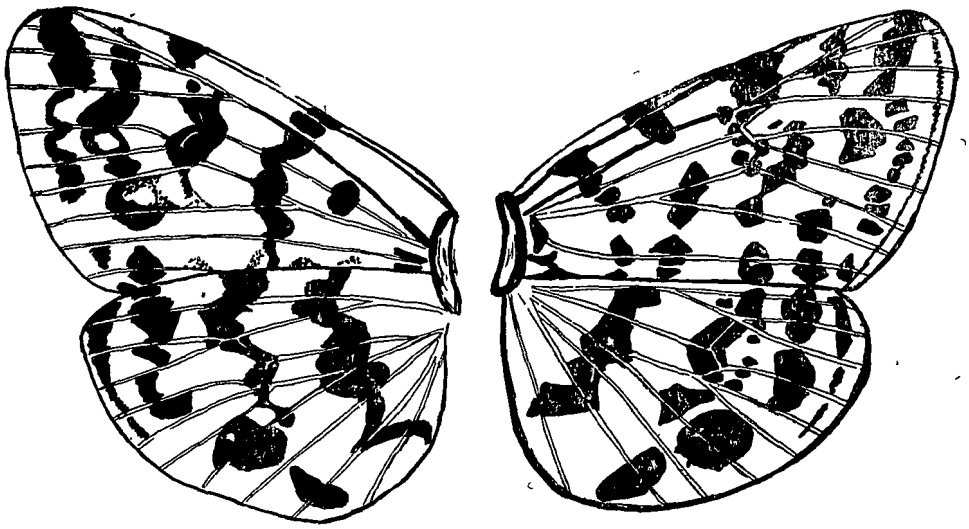

Fig. 2. Rhyparia purpurata.

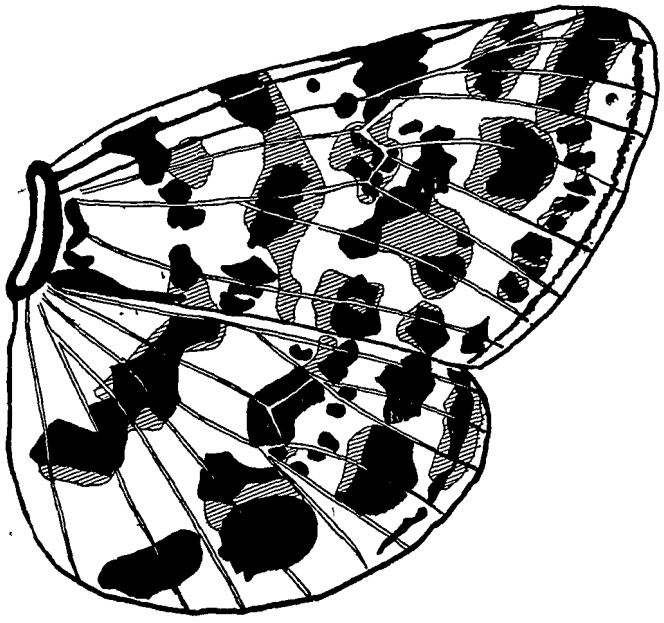

Fig. 3. Rhyparia purpurata (upperside in black, underside hatched).

Arctia maculosa and *Ocnogyna corsicum* var. *sardoa* also present good instances of regular rows of spots. In a still higher degree this is the case in *Deiopeia* (*Utetheisa*) *pulchella*, and here indications are found, that the original number of the transverse bars may have been even greater, these indications neither wanting in *Rhyparia*

itself. In *Deiopeia* for the rest the contrast between fore- and hindwing, and especially between upper- and underside, is still stronger than in *Rhyparia*, and the pattern of the under-surface shows fargoing modifications and discontinuities. Should my views, as explained in the foregoing, be right, then the upper side of e.g. *Coscinia cribrum* bears the traces of the seven series of spots in a more or less complete state, (especially in the variety *rippertii*), *Coscinia striata* on the contrary being more modified in this part of her colour-pattern, as in this form the rows of spots have coalesced more or less in a longitudinal direction and thus changed into coloured streaks filling the internervural spaces. Yet traces of two transverse rows of spots can still be clearly distinguished, represented by a submarginal row of more or less independent, dark, internervural streaks, and by the discoïdal spot. The latter remains in existence, even when the remaining design completely vanishes, as is also the case on the hindwings and the underside of both wingpairs.

In this way we are led without difficulty to the supposition, that the colour-pattern of Arctiidae should be deduced from an

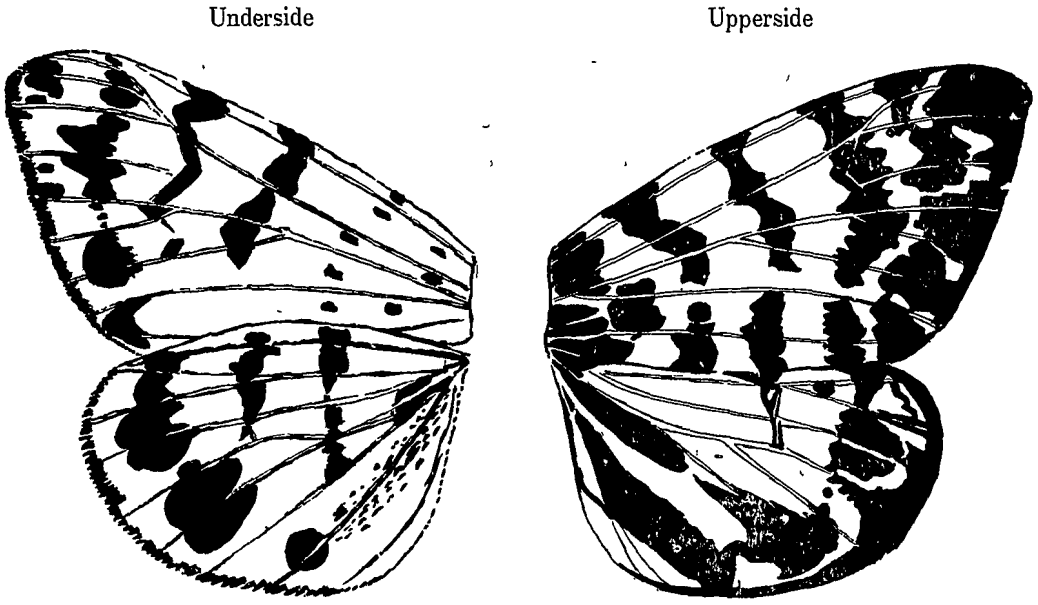

Fig 4. Ocnogyna corsicum, var. sardoa.

ancestral fundamental form, in which a light ground is dividedi nto seven fields by a corresponding number of transverse rows of dark spots. These rows run uninterruptedly from fore- to hindmargin, on both sides of the fore- as well as of the hindwings.

The question however arises: is this ancestral form really the

representative of the original condition of wing-marking, or has it in its turn arisen by modification from a still more primitive pattern,

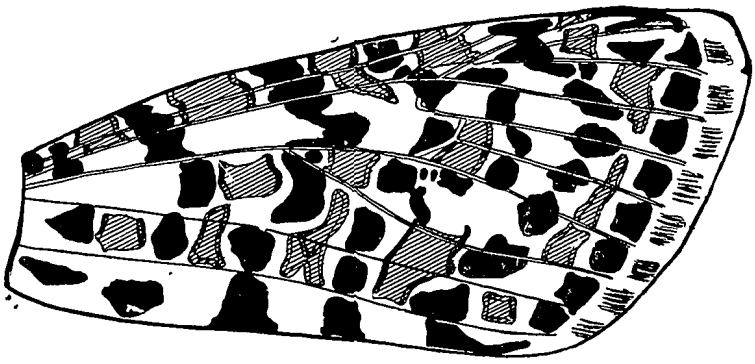

Fig. 5. Utetheisa (Deiopeia) pulchella.

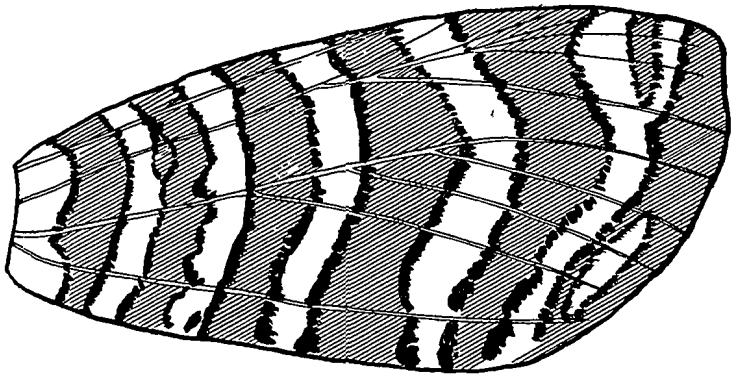

Fig. 6. Carcinopyga lichenigera.

in which the transverse rows of spots were still more numerous. The abovementioned traces of an originally higher number of spots in *Uthetheisa pulchella* already points in this direction, but the supposition is especially supported by a comparison with the *Hepialids*, in which the number of rows, composing the dumbbell- or hourglass-pattern, which I consider as the primitive design, is nearly twice as large.

Should my supposition prove right, then the colour design of Arctiidae (as well as of numerous other Heterocera and probably also Rhopalocera) should not be considered as a representative of the primitive Lepidopterous pattern, but on the contrary as the homologue of the secondary Hepialid design. The latter in its turn has issued from the primitive one by higher differentiation of alternative rows of spots, e.g. of the rows 2, 4, 6, 8, 10, 12, 14, if, for convenience sake, we infer for a moment, that the original number really amounted to fourteen.

Now coming to the question, if still more indications of this original design can be found in the family of Arctiidae, the answer, in my opinion may be this, that here and there traces of it can be discovered, though very incomplete and indistinct. *Spilardia* (*Diacrisia*) *multiguttata* (Seitz. Vol. X, Taf. 22), *Pericallia ricini* (ib. X 25*a*), *Alphaea fulvohirta* (ibid. X, T. 25) show a division into ten alternately light and dark areas along the front side of the median vein: in the first species the dark parts wear the character of spots, in the latter the light ones. The increasing of the number is the consequence of subdivision of three out of the seven spots along the front margin.

Moreover the question may be proposed, if the variegated pattern in black, white and red, as occurring on the front wings of *Utetheisa* (*Deiopeia*) *pulchella* and other species of this genus, might possibly be founded on an original repartition of the wing-field into a number of bars twice as large as that indicated by the rows of black markings.

According to the ingenious supposition of DE MEYERE, the red markings in this pattern represent the groundcolour, while the white spaces should be considered as light courts around the black spots, these courts having coalesced so as to form a white mazework surrounding the red patches. It cannot be denied that this inference finds a powerful support in the design on the forewings of another Arctiid, scil. *Argina cribraria,* where the black spots on the yellow ground are surrounded by light courts, which but rarely enter into connection with each other, and are totally absent on the underside, as they also sometimes are on the superior surface, and always on both sides of the hindwing, whose design is for the rest quite similar to that of the forewing.

But in *Utetheisa* we are struck by the fact that on the borderlines between red and white spots brown demarcation-lines occur, which contribute to their character of independent spots with a specific form. Moreover in a few cases red spots are found to be divided into halves by a similar brown median bar. This makes me doubt, whether DE MEYERE's conception of this and similar colour patterns gives a clear and complete insight into their real nature. For I think it risky to start from the supposition that the colour pattern of Lepidoptera-wings should be composed of a groundcolour, serving as a ground against which markings of another hue stand out. According to my view no fundamental contrast exists between ground colour and markings; they have a common origin and become modified in the same way, by similar influences.

This view can be backed by numerous arguments. First it is seen in several groups of moths and butterflies that the light and dark shades are substitute for each other, some species showing dark spots on a light ground, others near akin to them light spots on a dark one. Obviously the connection between these two cases is not such that the dark spots in the species of the first group have grown light in those of the second, while the light ground colour at the same time darkened, but quite the contrary, that the dark spots grew larger and entered into connection with each other, thereby forming a network in which the remnants of the light ground-colour remained as isolated spots. Compare e. g. *Rhyparia purpurata* with *Callimorpha dominula* and *Arctia villica*.

In the same way as rows of spots can coalesce and form bars, the dissolving of the original design may proceed further and lead to complete selfcolour. An intermediate stage in this process is formed by the coalescence of part of the markings so as to form a groundcolour, while the rest of the spots stand out against it.

Neither does there exist a fundamental difference between light and dark colouring matter: black spots in one species being represented in an allied one by such of an identical shape and place, but of a different hue.

Generally this change in the shade of spots does not occur simultaneously over the whole of their surface, but starts from their centre and spreads to their circumference, this giving rise to annular spots with a light centre and a dark ring. In the genera *Ecpanthieria* and *Halesidota* all stages of this transformation may be found side by side in one and the same individual, and on comparing various specimens of the same species, it appears that the identical spot is entirely dark in one, annulated with white core in the other. Nor can arguments be detected for ascribing a different character to dark spots with a light ring, as in *Argina*, in comparison to light spots with a dark one. Consequently in my opinion, when considering the genesis of wing design, no plausible reason can be found to distinguish between spots of a more active behaviour in the transformation of the pattern, and a ground colour that plays a more passive rôle. In the Hepialids for instance the pattern is formed by the regular alternation of biconvex and biconcave spots, forming what I have called the OXO motive of wing design, these spots being equipotential in so far as they undergo similar modifications in colour, size and arrangement, under the influence of identical causes.

So I cannot agree with DE MEYERE's view, who considers the O-spots as the markings, the X-spots however as the areas of ground

colour, spared out between them. To assign a special character to part of the design is a matter of view or impression. Now examining the wings of those Hepialids that show the highest regularity in their markings, (e.g. species of the genus *Charagia*), with an impartial eye, we find that not the lighter O-spots, but quite on the contrary the darker X-spots make the impression of being independent positive elements of the design, between which the first mentioned appear as areas of a ground colour. Especially strikingly this is shown by the male of *Ch. mirabilis,* where in contrast to the female, the X-spots have grown into larger and more complicated markings, which I have compared to perforated cotton-plugs. Yet it may be stated, that likewise in the female those X-spots which belong to the secondary pattern, possess a well-pronounced independent character, as their colour in comparison to those of the primary ones has increased in deepness, hue and lustre. Though in a lesser degree, the same may be said of the O-spots on either side of those modified secondary X-spots.

Furthermore we see in the variety *chrysomallon* of *Ch. ramsayi* the spots of the primary pattern all melted together into a smooth ground, on which those of the secondary one stand out with great distinctness, these latter thereby forming a new pattern that possesses a great deal of similarity to the so called primary pattern of Arctiids. This comparison therefore gives a certain amount of probability to the supposition that the background on which the Arctiid pattern stands out, owes its origin to the coalescence of a number of separate spots, this ground-colour-formation being nothing more than a special case of self-coloration.

My views seem to me to find a support in the conditions of the colourpattern in the family of *Hypsidae*, so nearly alien to the Arctiids that many Lepidopterologists consider it as a subfamily of this latter group. Species of the genus *Agape* belonging to this subfamily show a number of dark spots along the proximal part of the frontmargin of the forewings, at regular distances of each other. Supposing these spots to occur along the whole length of the margin, their number would exceed a dozen, so they might perhaps be considered as remnants of the primary pattern.

No less remarkable and instructive is the complete design, in the female of *Agape orbicularis,* where the wing-field of both fore- and hindwing is divided by the colour design into two absolutely different parts. In this instance the upper- and underside are almost though not wholy alike, the first is somewhat more differentiated, the latter here and there is made diffuse by partial melanism. Com-

parison with the male and with allied species gives the impression, that the proximal pattern, consisting of dark spots on a light ground, has been driven back in the direction of the wing-root by the distal one, which shows the wellknown type of the filling up of the internervural cells by dark pigment with a light median streak. (Also DE MEYERE uses the term supplanting to this case). For a comparison of the stages of this phenomenon I point to the series *remigera*, *subfascia*, *cariae*, *producta*, *septentrionalis* among others (Seitz. Vol. X, T. 27).

Ultimately the proximal pattern must totally give way to the distal one (*butleri*, *proxima*, *eugenia*, *fuscipennis*, *bhawaua*, *papuana*). In one single case however (*octrealis*) the proximal pattern extends over the greater part of the forewing, the distal one only leaving traces of its presence along the outer margin.

The hindwing shows a greater tendency to lose all traces or nearly so of the distal pattern, its colour design thereby being restricted to the usual dark spots, arranged in concentric transverse arches in different numbers, on a light back ground.

Groningen, November 1917.