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Zoology. — *"The interrelations of the species belonging to the genus Saturnia, judged by the colour-pattern of their wings."* By Prof. J. F. VAN BEMMELEN.

(Communicated in the meeting of May 3, 1919).

In his Handbook of Palaearctic Macrolepidoptera STANDFUSS says on p. 106, at the end of his passage on the relative age of the three species Saturnia spini, pavonia and pyri: "If we exclusively paid attention to the imagines, much might be said in favour of the opinion, that spini is older than pavonia. For both sexes of spini, and likewise those of the new species from Kasikoparan (S. Cephalariae Ch.) discovered as late as 1882, possess a remarkably uniform type. From this type the male of S. pavonia sharply deviates, this species thereby appearing as recently changed in its imaginal dress. But as to the question if we should place the origin of Sat. pyri before the evolution of these minor forms or after it, the imago of this latter species does not seem fit to allow of a really certain conclusion.

In regard to the caterpillar- and pupal-stage, however, things are different. For these it can be clearly proved that S. spini, pavonia and pyri form in many instances three different degrees of protective resemblance against certain hostile factors of the outer world. In this scale everywhere spini occupies the lowest, pyri the highest degree. Keeping in view the excessively near relation and the great similarity of biological conditions between the three species, we are obliged to assume that spini came into existence before pavonia, and pavonia before pyri, or, using the scientific expression for these relations: that phylogenetically spini is the oldest, pavonia a younger, pyri the youngest form. For it evidently would be absurd to assume that in a series of so intimately related forms, the more perfect living being should have originated at an earlier date than the less perfect one".

These considerations of STANDFUSS induced me to compare the wing-markings of Saturnine-species, as well among themselves as with those of related genera, to see if this line of investigation did or did not lead to corresponding results as the inspection of the caterpillars.

In accordance with the general rules for the character of the wing-markings, which I thought myself justified in proclaiming, and which I tested as to their applicability to such families as Hepialids, Cossids, Arctiïds and Sphingids, I came to the conclusion that not pyri but pavonia should be considered as the oldest form. For in pavonia the festooned submarginal transverse lines and bands deviate less from the outer wing-margin and also show a smaller difference between their anterior and posterior extremity, the submarginal band therefore having the simplest and least irregular type. In the same way the difference between fore- and hindwing, as well on their upper- as on their underside — and therefore also between the superior and inferior surface of each of the wings for itself —, is smaller in pavonia than in the two other species.

In comparison to other Bombycids and to the remaining families of Heterocera, the colour-pattern of pavonia shows a greater similarity to the general primordial pattern of seven dark transversal bars, which I deduced from the comparison of all these forms, than the two other Saturnids. It might seem that this assertion is contradicted by the fact, that in pavonia the male at first sight looks entirely different from the female by its colour as well as by its inferior size, a difference which has apparently made a deep impression on STANDFUSS. But on nearer inspection and consideration the difference is by no means so important as it looks, and need not be regarded as of high importance. For the difference in hues is evidently connected with the frequently occurring feature of discoloration (i. e. partial self-colour) by which on the superior surface the hindwing has partially turned into yellow, while at the underside the same hue has spread over the proximal part of the forewing. On both wings this discoloration is accompanied by a slight and incomplete fading of the pattern.

Moreover it may be doubted, on very sound arguments, if the yellow hue — apart from its spreading over the dominion of spots and stripes, which are rendered more or less invisible by it — should be considered as a secondary modification of an older and more original hue, which latter therefore should have persisted on the upperside of the forewing and on the underside of the hind one. For this yellow-brown hue is characteristic for quite a number of Bombycine moths belonging to different genera, and in so far impresses us as a very original colour. It might therefore be assumed, that its occurrence in the male of pavonia should be considered as a reversion to an older condition, instead of being the appearance of a new hue.

But we may safely leave these questions unheeded, for the hues in which a pattern is executed, need not be taken into consideration, neither in this case nor in others, when judging the character of the pattern itself.

Now, if we carefully compare the markings of the male with those of the female and pay due attention to the half-vanished stripes and spots under the overspreading yellow, it becomes clear, that down to the minutest details, male and female agree in pattern. No more is there any necessity to consider the sexual dimorphism as an important progressive feature, by which p a v o n i a should distinguish itself from s p i n i and p y r i, and be characterised as a recently and strongly modified form, in contrast to the other two, which would have remained more conservative. For secondary and tertiary sexual differences occur in all kinds of Lepidoptera, as well as in other insects. In the Bombycine moths this feature shows itself in a remarkably high number of forms. Now have we really to consider each of these cases as a separate and independent deviation from a common original condition, in which male and female were alike in shape, size, hues and pattern? Or did the phenomenon of sexual dimorphism already show itself amongst primitive Bombycidae, in the days when the difference between them was less considerable than at present, and they still counted fewer specific and varietal forms; dimorphic species therefore then existing side by side with monomorphic as well as now. In this case the sexual dimorphism of p a v o n i a might repose on the manifestation or the permanency of an old hereditary disposition.

But even apart from this question, which can hardly be solved with certainty, it remains doubtful, if the species p y r i and s p i n i should really be considered older than p a v o n i a, on account of the similarity of their sexes. For I by no means consider it as proved, that in p a v o n i a the male, which deviates from the general hue of the genus, may be considered as the modified form, while the female, which seems to show so much more similarity to s p i n i and p y r i, may be regarded as the unchanged form.

When the general rules for the colour-pattern are blindly applied the solution of this question might seem easy enough. In the female of p a v o n i a as well as in both sexes of s p i n i and p y r i the fore- and hindwings on their upper- as well as on their underside, show the same clear whitish hue, here and there overspread with a black sprinkling, and subdivided into fragments by nervural and transversal straight or undulating lines. But this

general clear tint, reigning over the whole extension of the wings, as well as the similarity in design between fore- and hindwings, upper- and underside, impresses me as a secondarily acquired uniformity, rather than as a really original feature.

In my opinion we meet here with a similar case as in the wholly selfcoloured butterflies e. g. Gonepteryx rhamni or Aporia crataegi, in which without the least doubt the uniform hue is the consequence of the simplification of the shades, hand in hand with the total or partial regression of the markings. Still more striking is the similarity with the Parnassine butterflies (which, it need hardly be said, is of course wholly superficial and occasional). For in these as well as in Saturninae a set of highly differentiated eye-spots on the forewings, but still more pronounced on the hindwings, form the most conspicuous part of the pattern, though it may undoubtedly be taken for granted that the spotted design of the Parnassines has developed from a far more complete array of simpler and more uniform markings, such as are seen in Thais polyxena and its consorts.

As soon as we consider the similarity of fore- and hindwing, upper- and underside of the female of pavonia and of both sexes of pyri and spini as secondarily acquired characteristics, there need no more be any objection against the supposition that the male of the first-named species is more original than the female.

From this point of view we may further remark, that the existing contrast between the yellow upperside of the hindwing and the greyish one of the forewing, on which the markings are less hidden under the ground-colour, corresponds in a higher degree to the general type of butterfly-design than does the exact similarity of fore- and hindwing, the overwhelming majority of Lepidoptera showing a similar difference between fore- and hindwing.

In the fact that the discoloration (in this case yellowing) occurs on part of the *upper*side of the *hind*wing and of the *under*side of the *fore*wing, the male of pavonia is in harmony with both sexes of Smerinthus ocellata and of many other Lepidoptera. Up to a certain degree the frequent occurrence and similar extension of this discoloration can be attributed to the influence of the resting attitude of these moths, the discoloured areas being exactly those which during this attitude remain covered by similar parts of the adjoining wing. In his paper: "Sur la position de repos des Lépidoptères", J. T. Oudemans has directed our attention to this circumstance and expressed his opinion that during the development and modification of the colour-pattern in the course of time, the

hidden and the exposed parts had independently proceeded each along its own course (p. 81—83), on which the one as well as the other could get on at a higher speed and so reach a stage more remote from the original common condition.

From a general point of view I feel inclined to join this opinion, but in the case at hand it brings us little light. The difference between the covered and the exposed wing-areas in the attitude of rest, already slight in the male of pavonia, is quite insignificant in the female, as well as in both sexes of pyri and spini. The wing-markings on these areas seem not to be influenced to any notable degree by the habit of passing the forewings over the greater part of the hindwings during day-time. That traces of such an influence are still visible in the male of Sat. pavonia, might be taken as an indication that the original influence of the said habit is now gradually losing its force.

The highly conspicuous eye-spots in my opinion must have evolved from simpler discoidal marks, hand in hand with the above mentioned change in the influence of the resting attitude. This is already proved by their very different degree of differentiation in the several species of the genus Saturnia and of kindred genera. Eye-spots moreover always are special differentiations, secondarily developed on the base of a more primitive and simple colour-pattern, whose elements have occasioned them by modifications in the original shape, colour, size and direction.

In my previous paper, on the wing-markings of Sphingides, I tried to prove this assertion for the case of Smerinthus ocellata, in the same way as I formerly did for the Hepialid moth Zelotypia stacyi. It must however be possible to prove it as well in other cases, e.g. for Vanessa io and many other Nymphalids, and likewise for Satyrids and Lycaenids. Cynthia for instance shows in what way eye-spots and simple spots alternate in the row of submarginal markings, and also often how an eye-spot on the superior surface is represented by a common one on the underside. The difference between the two seasonal forms in the first place depends on the contrast in the differentiation of the eye-spots: in the dry-monsoon-generation they are scantily developed, in the wet-dito highly so.

Now, do the hybridisations of STANDFUSS throw any light on these questions? As far as I can see not much; in general the hybrids are intermediate forms, but as to the width of the submarginal dark seam, they agree more with pavonia than with spini, and assuredly far more than with pyri.

But in my opinion in order to judge about the interrelations of the colour-patterns of Saturnia, it is absolutely necessary to compare with each other as many different forms as possible, just as in the case of other groups of Lepidoptera. It certainly cannot stand criticism to draw consequences from the exclusive consideration of three intimately connected species as to the relative age of their colour-patterns.

When pursuing this broader way, the well-foundedness of the above-mentioned assertion, viz. that the colour-pattern of Saturnids is a special case of that of Bombycids, and the latter again of that of Heterocera in general, is clearly proved. To begin with: next to the three above mentioned species stands Saturnia (Caligula Jordan) boisduvalii, on whose upper side the submarginal dark seam broadens from before backwards in still higher degree than in pyri, which reduces the somewhat median clearer area under the eye-spot, (broadest in pavonia) to almost nothing by forcing it back in proximal direction.

The two dark borders by which this area is limited (and which I suppose to be V and VI) are in one place locally connected by a black transversal link. This part of the pattern of boisduvalii therefore shows the greatest similarity with the corresponding area of the pattern of the male pavonia, but in the latter the connecting link seems to run between IV and V. Generally speaking, it is not easy accurately to make out the exact consecutive number of the bands for each separate form, yet the comparison of the superior surface of the different species leaves the general impression, that the posterior broadening of the dark submarginal area is brought about by the progressive darkening of the colour in a proximal direction, which consecutively incorporates the dominion of a more proximally situated transversal bar. In the female of pavonia this darkening process is restricted to the area of Bar II, in the male it has advanced unto III, in the same way as in both sexes of spini, in pyri it has reached IV, in boisduvalii V.

On the inferior surface the broadening of the dark area proceeds more slowly and more equally over the whole extension of the dark submarginal field. Consequently the underside of spini e.g. resembles both the upper- and the underside of pavonia to a higher degree than its own superior surface. On the hindwing the backward broadening of the dark submarginal border is less pronounced than on the forewing, and this edge is there separated by a light-coloured band over its whole length, from the dark festooned line, that runs along the distal side of the eye-spot.

On the underside however (which is never represented even in large illustrated works) we again meet with the same feature, as mentioned just now for p a v o n i a, s p i n i and p y r i, viz. that the course of the transversal bars is far more regular and original than on the upperside, this bringing about a much greater similarity between fore- and hindwing on the first mentioned surface.

I want to draw your attention to a simple dark transverse stripe on the middle of both wing-pairs, almost devoid of incurvations and rather faint. On the forewings this stripe runs along the distal border of the eye-spot, on the hindwings along the proximal one. Regardless of this difference, I think we have to deal in both cases with vestiges of bar IV. To this assumption I am especially led by the comparison of the upperside: On that of the forewing the anterior part of this bar is quite apparent up to the eye-spot, which constitutes a marked difference between b o i s d u v a l i ï and the three first-mentioned species. Past the eye-spot however the posterior part of the bar is wanting, but from the postero-interior border of that spot a black stripe runs across to Bar VI, turning sharply at an angle in the middle of its course and then running parallel to Bar VI, perpendicularly to the posterior wing-border and as far as this latter. The lastnamed part belongs to Bar V, as is proved by its comparison with the upperside of the hindwing, on which the Bars IV, V and VI may be perceived in their full extension, though faint and half-hidden under the hairy coating.

On the underside of b o i s d u v a l i ï therefore the dark submarginal border of both wing-pairs is located between Bars II and III; on the upperside however this is only the case on the hindwing. Bar III may even remain separated from the dark seam as an independent isolated stripe, as is shown in the illustrations of Seitz (Vol. II Pl. 31[a]), in contrast with the specimen at my disposition, where the black internal border was not free from the much broader marginal seam.

In some respects S a t u r n i a (N e o r i s Moore) s c h e n c k i ï corresponds with b o i s d u v a l i ï, e.g. in the presence on its underside of an extremely faint yet complete transversal stripe, which takes its course along the eye-spots. In this species however no difference exists as to the situation of this stripe on fore- and on hindwing, while the stripe is also present on the upper-side, though in an incomplete and unequal way.

Bar V is here the most pronounced and regular, VI and VII are hardly visible.

The eye-spots have been removed outward, and in consequence

the dark submarginal seam has been reduced, while Bar II and III cannot be distinguished from each other. They are represented by a single dark double-line, which in its anterior part is very much festooned. At the outer side of this double-line a white bar runs along, followed by a particularly broad margin of a light-manilla brown hue.

The comparison with the female pavonia makes it probable, that the dark submarginal edge ought to be situated between the white bar and the dark double-line, and that therefore we may assert that it is absent. Yet this is true only to a certain degree: the broadening of the dark submarginal border is, as we remarked before, a consequence of the advancing of the obscuration over the areas between the succeeding transversal bars in a proximal direction, and this identical process is also seen to take place in schenckii, viz. on the fore-wing between double-line II + III and the dark stripe representing IV.

At the underside of schenckii the pattern is simple, and moreover pale and reduced.

A.o. the eye-spots on the hindwings are much smaller, paler and less complete than at the upper side.

Amongst the many genera near-akin, that are arranged around the Saturnids, a great number of additional arguments may be found for the above-mentioned assertion, that their colour-pattern may be derived from the same scheme of seven dark transversal bars, which proved applicable to Arctiids.

We only need point out forms like Rhodinia fugax, probably showing II, III, and V or VI, or Laepa damartis (SEITZ II, Pl. 32[d]), which on its forewing wears I, II, III and V or VI, on its hind-wing I, II, III, IV and V (the last two only in part). Even in such a complicated and special pattern as that of Brahmaeids it is comparatively easy, with a little attention, to find again the seven primary transversal bars.

However it is not only the ground-plan of the wing-design that may be shown with great probability to be common to numerous and various groups of moths, also the modifications of this plan seem to take place after the same rules among the different families of Lepidoptera. In the present case of Saturnine moths it is the broadening of the submarginal dark border in the direction of the hind margin, that constitutes the principal difference in pattern between the various species mentioned and leads to their arrangement in the sequel: pavonia, spini, pyri, boisduvalii, while the pattern of schenckii seems to be due to a secondary regression of the dark band on its forewings.

This broadening in a caudal direction makes the impression, that an oblique line of separation runs across the forewing from tip to root, dividing it into an antero-interior lighter field and a postero-exterior darker one. Calling this line the *V*-diagonal (because the lines of the two wings in expanded attitude form the letter V) we may state, that this *V*-diagonal-design occurs in numerous Lepidoptera of various families, though always as a secondary modification of the original pattern of transversal bars. In the group of Chaerocampine Sphingides, which I hope to discuss in a future communication, this feature is particularly striking.

We find it however in the same way in the families of Hepialidae, Noctuidae and Geometridae, and likewise in numerous Microlepidoptera. In the overwhelming majority of these cases the *V*-diagonal-pattern is restricted to the upper side of the fore-wing; the underside showing the primitive pattern of transversal bars.

As specially striking examples may be mentioned the Noctuid genera Ophideres, Nyctipao and Emmondia, the Bombycid genus Eupterote, as well as many Geometrids.

The species of Ophideres give rise to the remark that the separation of the forewing-area in an antero-internal and a postero-external part, brought about by the *V*-diagonal-design, in many species e.g. O. tyrannus, salamia and fullonica (comp. Seitz III, Pl. 66) seems to be connected with the resemblance of the entire forewing-design to a withered leaf, this likeness bringing the said species under the category of the leaf-imitating Lepidoptera.

We have to deal here once more with such a feature, as can show itself in many different shapes, and therefore in its real character is evidently independent of the importance it may in some particular cases possess for the establishment of protective resemblance.

It further results from the mutual comparison of different species, that the contrast between the anterior and the posterior part of the wing-surface may be very different in quality as well as in quantity. In some species the forepart is light, the hindpart dark, in others they are nearly alike. In O. materna a transversal design of Cossid-markings (traits effilochés Botke, Rieselung Eimer) spreads over both parts; in the male the *V*-diagonal is present, in the female absent, while on the contrary an *A*-diagonal-design is partly developed as a light-coloured-streak. For besides the *V*-diagonal an *A*-diagonal can be distinguished, running from before and inside to behind and outside in an oblique direction over the wing-surface, often it seems to possess some connection with the division of the

wing into a beam- and a fan-part (Spreiten- und Faltenteil -as SPULER has termed them).

In the species Miniodes discolor, near akin to the genus Ophideres, the dark *A*-diagonal separates the orange-coloured forewing-area into two parts: both of them well showing the Cossid markings. A remarkable detail in this case is the uniform pink colouring of the hindwing on its upperside, the under one showing just the reverse: self-coloured forewing, Cossid markings on the hind one.

On the upper-side of Nyctipao crepuscularis (SEITZ III, Pl. 58) markings in three different directions cooperate to form the pattern: 1. transversal markings, especially the white line running from the anterior to the posterior margin through the centre of fore- and hindwing, but also the dark bar near to the wing-root, representing Bar VI or VII, 2. the *V*-diagonal designs of the forewing, 3. a white stripe, forming an obtuse angle with the *V*-diagonal, and running parallel to the *A*-diagonal. Inside the angle, made by the *V*- and the *A*-diagonals, an eye-spot has been differentiated from elements of the transversal markings.

Still sharper these three directions of wing-markings stand out in dark bars against a creamy-white fond on the fore-wings of the arctiïd Areas galactina. So numerous are the cases of *V*- and *A*-diagonal-design, that I will not even venture to summarize them and compare them to each other. As a general result however of my comparative investigations, I feel justified to assert, that everywhere the secondary character of this pattern may be stated with surety, and that in the great majority of cases the underside shows no trace of one of these oblique lines, whereas clear vestiges of the seven original transversal bars nearly always occur, and are also frequently present on the upperside, though generally incomplete. In Rhopalocera the *V*-diagonal-design, when it occurs, is restricted to the underside, and here serves to establish the leaf-imitating character.

Groningen, April 1919.

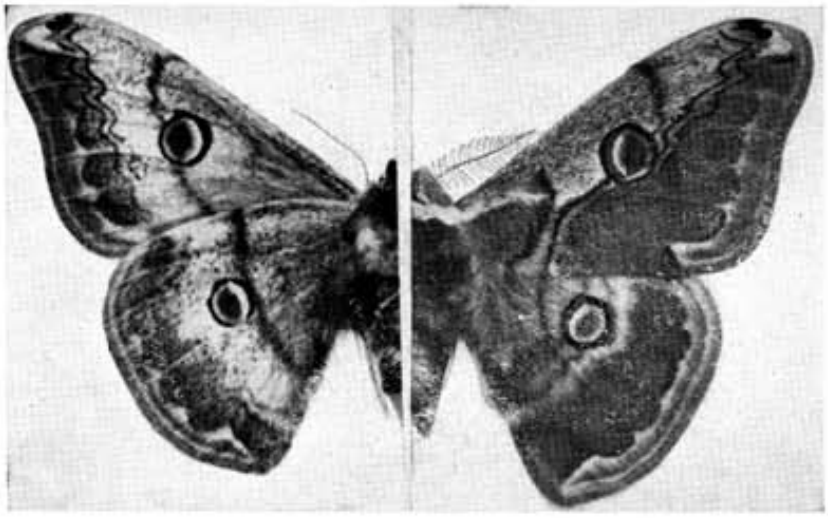

Fig. 1. SATURNIA BOISDUVALII ♂.

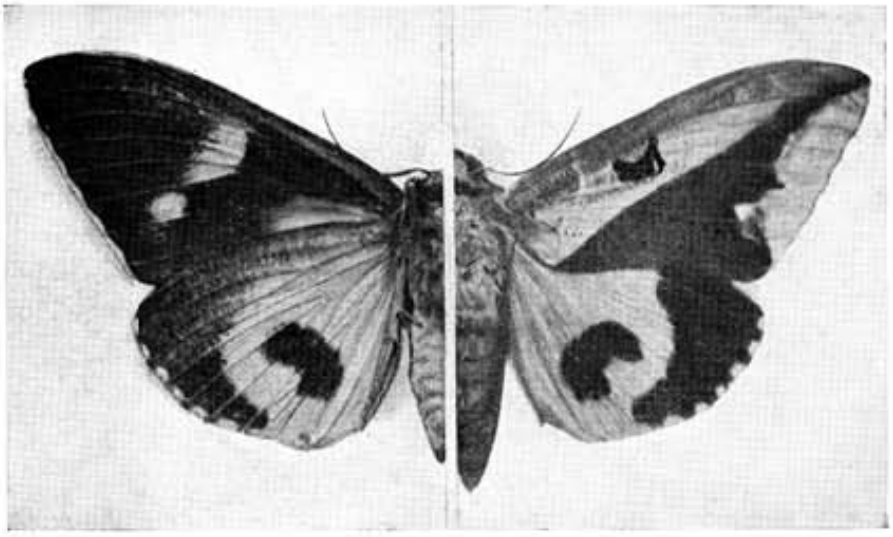

Fig. 2. OPHIDERES DIVIDENS ♂.

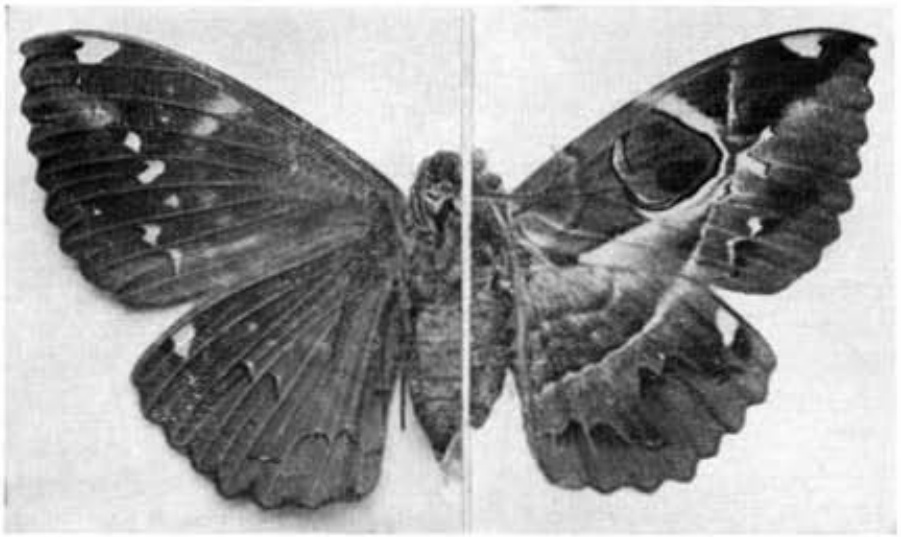

Fig. 3. NYCTIPAO CREPUSCULARIS ♀.

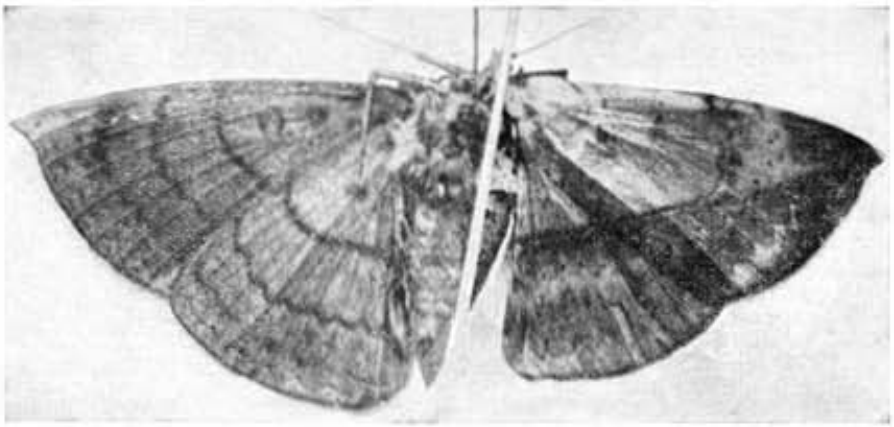

Fig. 4. EMMONDIA PUNCTATA ♀.

E. THEYSSEN, phot.