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Zoology. — “*The wing-design of Chaerocampinae*”. By Prof. J. F. VAN BEMMELEN.

(Communicated at the meeting of October 25, 1919).

In a monograph, which is now being published as a supplement to *Zeitschrift für Wissenschaftliche Insectenbiologie* von CHR. SCHRÖDER in Husum, and of which I received the first part a few months ago, Dr. P. DENSO, the author of *Palaearctic Sphingides* in SEITZ' *Macrolepidoptera*, begins a description of the lepidopterous hybrids that have hitherto got known, with considerations on the wing-design of the species of *Celerio*. On page 1 he says about this: “Thorough investigations and theoretical considerations, which it would lead me too far astray to reconsider here, clearly show that the markings (and hues) of all *Celerio*-moths may easily and without constraint be derived from a primitive form, which only very slightly deviates from the pattern still found in the oldest species of *Celerio*, viz. *zygophylli* O., or likewise in *lineata*, when we only abstract from the white striation of the wing-veins. It must be mentioned here, that the original design of the species of *Celerio* is nearly related to that of the more closely-connected species of *Pergesa*”.

I deplore that DENSO did not think fit to publish in detail his “thorough investigations and theoretical considerations” on the phylogenetic interrelations between the different species of *Celerio*.

For now we are obliged to deduce the grounds for his assertion “that *zygophylli* and *lineata* have to be considered as the (phylogenetically) oldest species” from a few remarks, which must be picked up here and there in the course of his paper.

Such being the case, I prefer first to expose my own views independently of DENSO's considerations and afterwards to discuss his deductions.

In my eyes the only way to acquire a trustworthy insight into the wing-design of *Celerio*-species, is to compare it with that of other genera of Sphingids, especially *Chaerocampinae*. When keeping this course, it becomes evident that their colour-pattern is a highly modified variation of the general ground-design of Heterocera-wings, due to reduction and obliteration of the general primitive set of seven transverse bars, by the influence of the *V*-diagonal-motive (this being the name which in my foregoing paper on the wing-pattern of *Saturnidae* I gave to the system of linear markings running

obliquely across the wing from tip to root). Consequently in my opinion the most original pattern must be looked for in those Chaerocampinae that show the fewest traces of this influence of the *V*-diagonal on the transverse bars. Now it is evident that this does not at all occur in *zygophylli* and *lineata*, but on the contrary in *Pergesa* (*Deilephila*, *Metopsilus*) *porcellus*, and better still in *Berutana* (*Metopsilus*) *syriaca*. In this latter the forewing shows a set of transverse bars which remarkably agree with that of *Smerinthus populi*, though they do not to any notable degree pass over upon the hindwing.

The *V*-diagonal is only very slightly indicated at the apex of the wing in the shape of the foremost external triagonal spot, which extends from the wing-tip along the front-border, and shows the form of a dark-brown threesided blotch, growing fainter and of lighter hue from before backward. It remains separated from the convex blotch along the external margin by a narrow space, which is occupied by the well-known oblique white apical stripe, that is seen in so many different forms of Lepidoptera.

In the same way the posterior triagonal spot is well-developed, but remains separated from the anterior one by three internervural spaces, containing only faint traces of dark marginal spots.

Bar II is complete and well-marked, III on the contrary hardly visible, IV is a broad dark band, imperceptibly passing at its external side into the area where III would have occurred, had it been visible, but very sharply traced at its internal border. V is rather sharp, but does not reach the back-margin of the wing. VI is just indicated by a faint trace, VII on the contrary is invisible.

On the upper side of the hindwing a broad marginal seam and an obscuration of the root-field are the only traces of the pattern.

On the inferior surface the common heterocerous pattern occurs, viz. a design which is the same for front- and backwing, and betrays clear traces of reduction, when it is compared to that of the upper-side. For it only consists of a well-defined marginal range of (coalesced) spots, inwardly bordered by an irregular zig-zag-line, and moreover of the bars II and III, represented by brown lines on a lighter ground.

The wing-design of *porcellus* may rather easily be derived from that of *syriaca*, and this deduction presents a certain amount of probability, as the complete set of seven transverse bars is clearly discernible along the front-margin of the forewing. Three of these bars: the outward or distal ones (I, II and III) reach the hind-margin.

When I call this pattern an original one, this expression should not be taken in the absolute sense generally connected with it.

Precisely in the case of *porcellus*, it can be proved in a very striking way, that this would be inappropriate.

For not only the pattern of the seven transverse bars is represented on the fore-wing, but that of the *V*-diagonal as well. Or expressing it in other words, we may assert that the pattern of *porcellus* could be obtained by combination of that of *Smerinthus populi* with that of *Elpenor gallii* and *euphorbiae*, of course under omission or reduction of certain parts of each.

The best proof for this assertion can be given by superadding the wing-patterns of the above-mentioned species to that of *porcellus*, or, otherwise, by marking with a darker hue those elements of foreign wing-designs in the *porcellus*-pattern that can be discovered in it.

Bar I, otherwise called the marginal seam, shows in *porcellus* the usual type of an irregularly indentated, wine-red streak, which is characteristic of Chaerocampinae. It begins at the wing-tip with the above-mentioned oblique white stripe, which likewise is of so frequent occurrence among Sphingides, and can be considered as the outmost fragment of the *V*-diagonal.

Bar II begins with a tolerably distinct, rather dark blotch, in the wine-red streak along the front-margin, but gets much fainter as soon as it enters the yellow-brown central area of the wing, which it traverses in a well-marked inward curve.

Bar III likewise begins at the front-margin with a double-blotch, but becomes a single band when entering the yellow area, and at the same time gets into contact with the discoidal spot, which itself may be considered as a remnant of Bar IV. Furtheron B. III runs parallel to II, both being dislocated a little in the direction of the wing-root.

V and VI are represented by a pair of small, greenish-brown stripes in the red field, VII can confusedly be traced in the brownish root-area.

On the upper side of the hindwing the only point of similarity with the forewing is formed by the wine-red marginal seam, but the underside once more proves, that also in *porcellus* well-marked remnants of the transverse bars occur in the shape of dark spots and stripes on the light-yellow and rose-red fond. As in most other cases these are especially well-marked along the front-margin.

At the underside the similarity between fore- and hindwing is again much more pronounced than on the opposite surface, the design on the firstnamed wing being more reduced than on the last, especially as regards the root-field.

The same red, violet and greenish-golden-brown hues that decorate

porcellus, are found back in *elpenor*, a great superficial similarity resulting from this, which finds its expression in the popular names.

But in the pattern an important difference prevails, for in *elpenor* the traces of transverse bars along the front-margin are almost completely absent, while on the contrary the *V*-diagonal design is strongly expressed, though in fact it reaches the back-margin of the wing in its more distal part, and therefore deviates in a lower degree from the original transverse direction of the primary bars than is the case with other Chaerocampinae.

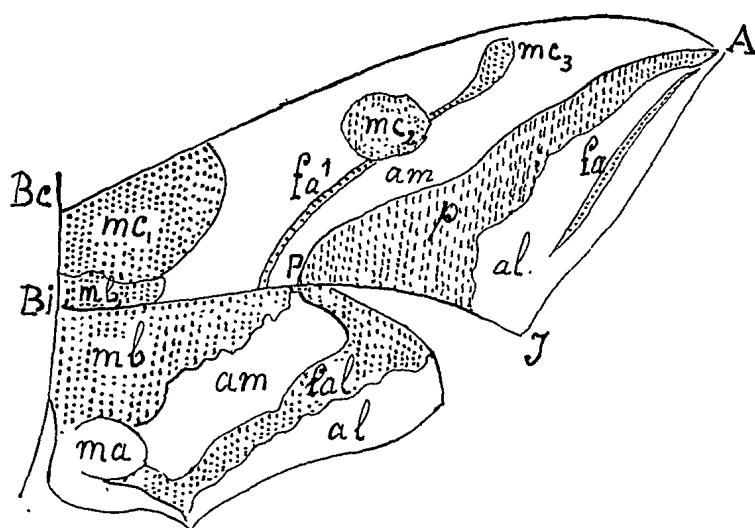


Fig. 1. (after DENSO).

DENSO pays special attention to this vicariating relation between the two parts of the back-margin of different species of *Celerio*, into which it is divided by the above-mentioned oblique line, which, starting from the wing-tip, forms the outer border of the light middle-field. He arranges these species in a series, beginning with *lineata*, where the meeting-point of this line with the back-margin lies farthest towards the proximal side, and ending with *nicaea*, which in its more distal position of this point more or less agrees with *elpenor*.

As far as I feel able to understand his views, he seems, for the just-mentioned reason, to consider *lineata* as more original than *nicaea*.

According to my conviction the relation between these two species, is precisely the opposite one.

To me it just seems remarkable that DENSO, when speaking of another detail of the wing-design, which he remarked in a few

specimens of *nicaea* only, comes to a conclusion that exactly agrees with my views. For DENSO considers the occurrence of a dark line over the middle part of the wing, which appears from time to time (called by him *fa*, and running parallel to his median bar *am*) as an atavistic phenomenon. Now this line can scarcely be anything else than Bar III of *porcellus*, and therefore in my opinion may really be considered as the reappearance of an element of the original design.

In truth this unexplainable confusion and contradiction in his views can be remarked in different passages of DENSO's contentions: e.g. when he says in describing the *lineata*-design: "my investigations led me to assume, that *lineata* and certain specimens of *zygophylli* show a design, that very nearly approaches the original *Celerio*-pattern. In fact, when drawing the contours of the *lineata*-design, they completely include the elements of the pattern of all remaining species of *Celerio*, these latter therefore appearing to be due to the more or less far-reaching reduction of the original design. This may be demonstrated by Fig. 2".

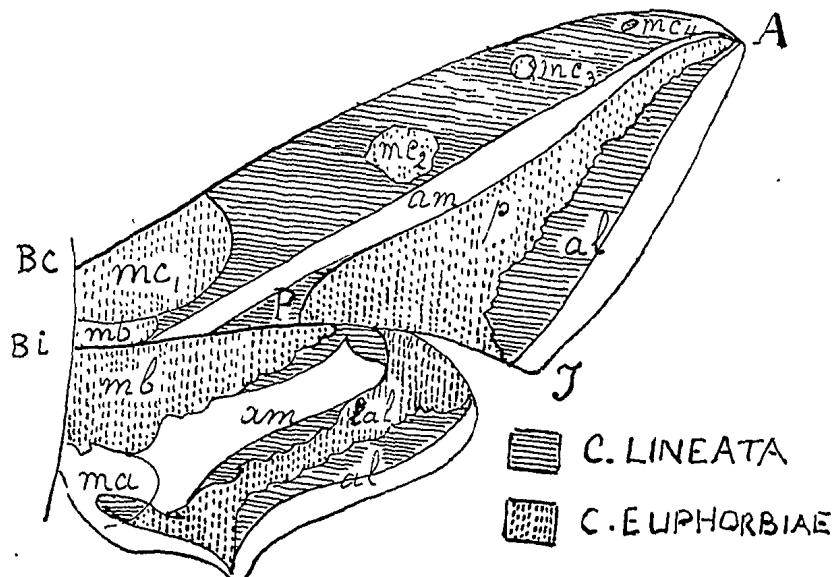


Fig. 2. (Copied after DENSO).

Now in this figure we remark, how *lineata*, besides showing the *V*-diagonal, possesses only a single vestige of a bar (*l*) along the external wing-margin, and therefore next to nothing of the original design, while in *euphorbiae* on the contrary the remains of at least four transversal bars are present along the front-margin, though in truth only in the shape of isolated blotches. Were we obliged to share DENSO's views, we should have to assume that self-colour is

the more primitive condition of wing-coloration, all patterns taking their origin from it by dissociation of the homogeneous hue into spots and bars.

This really seems DENSO's opinion, notwithstanding a few lines before he asserts: "As to the underside of the wings, we also here find, that progression in phylogenetic development always goes hand in hand with an increasing loss of elements of the pattern. *Lineata* is richest in details, *gallii* less so, *zygophylli* the same, while *euphorbiae* and *nicaea* show the fewest components of the pattern".

I see no need here to remonstrate that this assertion can as well be applied to the upper side of forms like *C. lineata* and *D. elpenor*, in comparison respectively with *C. euphorbiae* and *D. porcellus*.

Neither can I agree with DENSO's contentions (p. 5) about the "manifes-

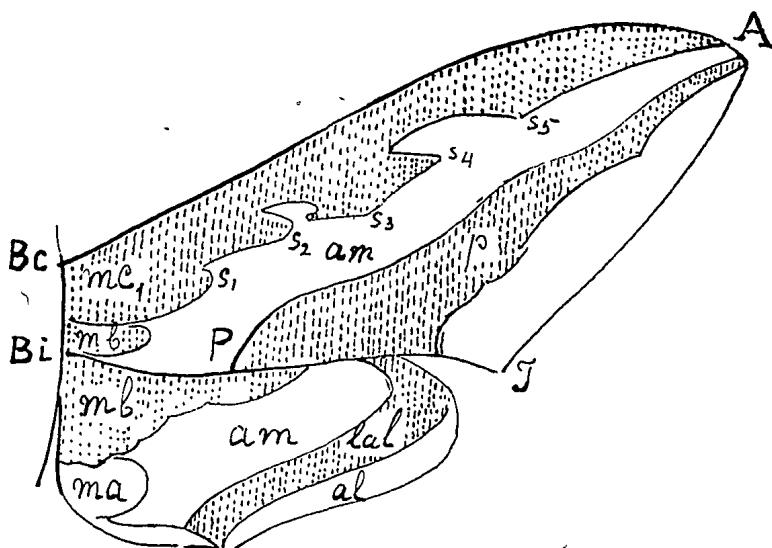


Fig. 3. (after DENSO).

tation of atavistic characters". He writes: "Very often we remark in pure species, e.g. *gallii* or *euphorbiae*, a dark, indistinct line, starting at the wing-tip near to the transverse bar *p*, and running parallel to the distal border, across the marginal field. In most cases this line is rather short, and disappears nearly halfway between apex and hind-corner; rarely it attains this corner and there joins with the bar *p*. It takes exactly the same course as does the distal bordering of bar *p* in *lineata*. Without doubt we here meet with an atavistic feature; it is nothing but the old borderline of the *p*-bar. In vain therefore should we look out for it in the *lineata*-group, while in *zygophylli* it will only occur on rare occasions and in a weak condition, as the regression of *p* has only just begun. *Gallii* often shows this line, *euphorbiae* more rarely, *nicaea* extremely

seldom, which can be easily understood, as the two latter, being relatively young species, have already long since lost this borderline of p'' .

Comparing the wing-designs of *gallii*, *zygophylli* and *livornica* (as figured in SEITZ, comp. vol. II Taf. 41. d.) I come to the conclusion that in the second of these species the line in question, *fa*, is present without exception, but that it has been dislocated a little towards the internal side, and moreover that this line is also present in *Pergesa oldenhamii* and *japonica*, and likewise in *Celerio boisduvalii* and *minor*, though its shade may differ in saturation.

For the rest I cannot well understand, why precisely this line should be of special atavistic importance; though on the other side it is of course beyond discussion that it has originated by the coalescence of the external row of spots (Bar I), which runs parallel to and in the immediate neighbourhood of the external margin of the wings. Nor am I able to see why there still should exist differences in the degree of atavism between the several transverse striae, which, according to DENSO occur from time to time as variations in the different species. DENSO himself seems inclined to accept this difference, for he says:

"In contrast to the line *fa*, which forms a feature restricted to forms within the limits of the genus *Celerio*, another atavistic line goes back to a far wider plan, viz. to elements of design also appearing in the genus *Pergesa*. I mean a dark line *fa₁*, which, beginning at the costal spot *mc₁*, runs along the costal zone *ac* and parallel to the proximal margin of *p*, towards the posterior wing-border. Very often this line forms a connecting link between the spots *mc₁* and *mc₂*. It only occurs in specimens, where the tendency to dissolution of the costal zone into separate costal-spots shows itself, or in which this dissolution has already been achieved, e.g. *zygophylli*, *vespertilio*, the *euphorbiae*-group and *nicaea*. Never on the contrary does it appear in *hippophaes*, *gallii* and *lineata*".

Judging from *vespertilio*, when compared with *askoldensis* and *mellus*, the line in discussion must be the one I designed as Bar III, but which here must have blended with IV, traces of this line being present not only in some, but in all specimens of *dahli* and *euphorbiae*, near to the posterior margin of the wing.

In accordance with these remarks, it is self-evident that my views about the wing-markings of the *euphorbiae*-group are absolutely in contradiction with those of DENSO. For this author says: "In *C. euphorbiae* L. the process of dissolution of the original *Celerio*-design has proceeded very far already".

I feel convinced that in this case a process of dissolution is out of the question, but that quite on the contrary we can still discover the last traces of the transversal bars along the front-margin of the wing, in the shape of isolated spots, the posterior and distal part of the wing meanwhile remaining under the dominion of the *V*-diagonal-pattern. Yet I am willing to admit, that the reduction of the transverse rows of spots to three or four irregular blotches along the front-margin (called by DENSO costal-spots) and the gradual diminution in size of these spots towards the wing-tip undoubtedly are in connection with the course of the *V*-diagonal, and that the entire set of these three or four blotches responds to the dark anterior marginal field of *C. lineata*. This latter area however I consider as a blending of those four blotches, i.e. as partial self-coloration, leading to uniformity of hue of the whole anterior marginal field. The justification for this way of regarding the question, I see in conditions as found in *C. gallii*, where the blotches, though in connection with each other, in such a way that the front border of the wing is entirely and uniformly dark-coloured, yet are perfectly distinct in their original extension by the occurrence of arcuate incisions from the side of the light diagonal middle *V*-bar.

That DENSO looks at this condition from an opposite point of view is revealed by his expression: "*Gallii* possesses a broad costal margin, in which the (light) groundcolour has *intruded*, (the italics are mine), especially from three points of the middle-area *an*".

The same considerations can be applied to the dark triangular area, which forms the postero-external border of the light diagonal bar, and which DENSO calls *p*. When speaking of *C. euphorbiae*, he remarks about this bar: "The proximal limit of the transversal bar *p*, in its hinder part, which touches the back margin of the wing, has been *removed* towards the posterior wing-angle". According to my view, it has remained at its original place.

Though his remarks about *gallii* are restricted to the words: "The bar *p* is broader than in *euphorbiae*. Its terminal point *P* is situated more towards the base of the wing", he declares in a preceding passage: "Starting from the distal border" (of the light median area) "the marginal coloration of *al* increases in extension at the cost of *p*, and moreover *an* broadens along the posterior wing-margin, thus causing the proximal limit of *p* to stand more perpendicularly to that margin".

Also in this regard therefore, DENSO's views are diametrically opposed to mine.

And yet I could see a possibility that DENSO's view of the matter

might after all prove right. For this would be the case, when we had to surmise, that in *gallii*, and still more in *euphorbiae*, the presence of the spots along the anterior wing-margin was due to reversion of the archaic pattern, i.e. to atavism. We then should be obliged to imagine that in the pattern of *lineata*, the uniform dark anterior region of the diagonal-pattern, itself derived from the coalescence of the anterior parts of the original seven transversal rows of spots, had again been solved into a certain number of free blotches. The fact that this number is lower than seven, renders some probability to the supposition that we have here to do with a secondary dissociation of an originally coherent longitudinal bar along the entire anterior wing-border. But according to my view the primary cause of this dissociation may be seen in the hereditary presence of the tendency to the formation of isolated marginal spots, belonging to the ancient pattern of transverse rows of maculae, which is common to all Heterocera.

When trying to analyse in this same way the complicated pattern of the upper-side of the forewings of *Deilephila (Daphnis) nerii*, we come to the conclusion that without constraint derivatives of all the seven transversal bands can be recognized in the alternately dark and light areas along the anterior wing-margin, but that only one of them, viz. V, runs on unbroken to the posterior margin, VI nearly doing as much, as it only becomes crossed by the white external seam of the dark root-field. The disturbances in the rest of the transverse bars may for the greater part be attributed to the well-known influence of the *V*- and the *A*-diagonal-design. The first manifests itself in the same manner as in *euphorbiae*, *gallii* etc., but in *nerii* only fragments of the light median bar of the remaining Deilephilas can be discovered. In the first place we remark the light apical marking, strongly contrasting to the extremely dark anterior segment of bar I. Then comes the white curved stripe in the middle of the posterior margin, abutting towards the median side against a peculiarly dark hinder part of a transverse bar (probably a fragment of IV) and which in its forward zig-zag-course gets twice abruptly broken. I presume that this characteristic white zig-zag-line represents part of the distal border of the triangular light central part, which broadens towards the hind margin and is so characteristic of Chaerocampinae.

For the rest this light central field is only represented next to the root-field by its most proximal part running along the posterior wing-border. This part narrows and describes a convex curve, thereby passing into the area of bar VI, and reaching the anterior margin. In the same way the light colour-party at the external border of V

advances distally towards the anterior wing-margin, and so comes in contact with the fore-end of a still lighter bar, which begins in the area of III at the said margin, but takes such a sinuous course in a postero-external direction, that the dominion of III so to say curves up to that of II.

A similar feature can likewise be observed in another Sphingid, whose forewing-pattern agrees with that of *nerii* in a remarkable number of points, viz. *Dillina tiliae*. Here the feature in discussion is seen in the anterior part of the external border-line of the dark central field, by which the forewing is so characteristically divided into a proximal and a distal light area, and which itself is broken up (either completely or nearly so) into a larger anterior and a smaller posterior portion by a constriction along the course of the second cubital vein. This constriction corresponds in position and character to the above-mentioned white zig-zag-line of *nerii*.

That this explanation of the forewing-pattern of *nerii* is well founded, becomes especially evident when we compare it to that of nearly-related species, e.g. *hypothous* (MOORE, Lepidoptera Ceylon, Pl. 83; CRAMER, Pap. Exot. III pl. 285 D; Seitz, X 63a), *layardi* (MOORE, Pl. 81; Seitz 63a³), *protrudens* (Novara Exp. Zool. II, 2, Taf. LXXVI, 7; Seitz X, 63b³), *angustans* (Nov. Exp. Zool. Bd. II 2), *placida* (Seitz, X 63a⁴).

But as the most remarkable patterns in regard to this feature I consider those of *omissa* and its congeners (*miskini*, *anceus*, *sericeus*, *cunera*), because here parts of the *nerii*-pattern are so to say projected on that of *Smerinthus populi*, the latter appearing as if it were visible by transparency beneath the first.

Groningen, October 1919.