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Zoology. — “*On the primary character of the markings in Lepidopterous pupae*”. By Prof. J. F. VAN BEMMELLEN.

(Communicated in the meeting of April 26, 1918.)

On p. 136 of his paper: Zur Zeichnung des Insekten-, im besonderen des Dipteren- und Lepidopterenflügels (Tijdschrift voor Entomologie, vol. LIX, 1915) DE MEYERE raises objections against the comparison of the pupal stage in Lepidoptera with the subimaginal instar of Agnatha; a comparison, which as far as I know, was first made by POULTON¹), and to which I have expressed my adhesion in my paper on the pupae of Rhopalocera²).

He says (translated by me): “It is well known that many investigators believe the pupa to have evolved from a flying imagolike form, the limitation of the wings to the last instar having been acquired later on. In these views I cannot agree with my colleague” (viz. VAN BEMMELLEN). “In what way one may imagine the initial evolution of the pupal stage to have taken place, either from a dormant subimago, or from a dormant larva (the latter alternative according to my view being the more probable), in any case I think to be justified in supposing that the Trichoptera, Panorpata, Diptera and Lepidoptera have differentiated out of Neuroptera, after the latter had acquired the Holometabolic metamorphosis they possess to-day. Now the Neuroptera generally have a faintly coloured pupa, which leads a hidden life, concealed in the earth or in a cocoon, and usually has a thin chitinous skin. Such also is the condition with Panorpata, Diptera, and likewise with a number of lower Lepidoptera, as Micropteryx, Lymacodides and many others.

When therefore we meet with special colour-markings exactly in the freeliving pupae of diurnal butterflies, I am inclined to regard this as a wholly secondary feature (The italics are mine).

This statement leads me to the following remarks:

¹) E. B. POULTON, The external morphology of the Lepidopterous Pupa, its relation to that of other stages and to the origin and history of metamorphosis; Transactions Linnean Society 1890—91.

²) J. F. VAN BEMMELLEN, Die phylogenetische Bedeutung der Puppenzeichnung bei den Rhopaloceren und ihre Beziehungen zu derjenigen der Raupen und Imagines, Verh. d. Deutschen Zool. Ges. 23 Versamml. 1913.

Against the use of the expression "subimago" in itself, for the pupal stage of Lepidoptera and other Holometabola, DE MEYERE does not seem to have fundamental objections, for as is seen from his own words, he declares that the pupa might be considered as an "inactive subimago," though he himself would prefer the name "inactive larva."

In this preference I cannot agree with him. The conception "larva" implies the presence of provisional organs, as well as the manifestation of a metamorphosis, the moment of which fixes the final point of larval life. Now it is clear, that this point lies at the passage from caterpillar to pupa. Therefore the latter cannot be called an "inactive larva", but only an "inactive subimago". It might even be asserted to represent an "inactive imago", for the provisional larval organs have disappeared, the imaginal organs on the contrary being all present, though still unable to functionate.

But it is especially against the inference, that this subimaginal stage should have been provided with a sufficient mobility to enable it to fly about, after the fashion of the caddisflies when they leave the water, that DE MEYERE raises objection. According to his view, it is much more probable that in none of their phylogenetic stages the Lepidoptera or any of their kin: Panorpata, Diptera, or Neuroptera, were ever on the wing before the very last moult, so before they fully deserved the designation "imago".

Now I must admit, that this supposition of the occurrence of a flying subimaginal instar among the ancestors of these groups of Insects is merely a hypothesis, which can only be supported by arguments of probability, while most assuredly important objections can be opposed against it. One of these difficulties I will indicate myself: Holometabolic Insects may indeed be compared still to other Hemimetabola than precisely the Agnatha, and moreover to Ametabola also, and this comparison may lead to raising the question, if the pupal stage might not best be compared to the last instar but one of these groups, to which belong insects, whose different instars are much more similar to each other than those of Holometabola, because all of them differ less from the imaginal condition, or, what means the same, because they have all deviated in a minor degree from the original Insect-type.

In them we see the wings protrude at an early stage as lateral outgrowths of the dorsal body-wall and increase in size at each following ecdysis, though entering into function at the last one only.

Why should this course of development be less primitive than that of caddisflies? Might not the curious phenomenon, that

the subimaginal instar of the Ephemeroidea, after moulting at the surface of the water, flies about for a few moments, then to moult again and immediately afterwards to proceed to copulation, rather be taken as a speciality of the Agnathous life history, without any deeper significance, and therefore of no importance for the explanation of Holometaboly with its dormant pupal-stage.

On this point I dare not pronounce a definite opinion, but should like to point out, that in trying to find an answer to the above stated question, we must take into account various general considerations, in the first place that of the development of wings in its totality, viz. the question how Insects (at least Pterygogenea) acquired their wings. For this decides about the question whether we are to suppose that the ancestors of modern Pterygote Insects never passed through a period, in which they moved about on the wing before attaining sexual maturity, or that the beginning of the functional activity of the wings (howsoever acquired) became more and more postponed to the last instar. If we are right in accepting the second alternative, and therefore in believing that the oldest winged insects could already make use of their wings shortly after their birth, the Agnatha may have retained a last trace of this ancient condition. The apparently absurd fact, that these animals fly about in their subimaginal coat for a few moments only, might then be explained by the assumption, that they gradually postponed the start on the wing to later instars, under the ever increasing influence of their secondary adaptation to life in the water. Then the difference between them and other Hemimetabola would not consist in a greater originality of the latter, but in a different mode of deviation from the primitive condition, viz. by the complete removal of the initiation of real flying to the imaginal instar.

The supposition of such a retardation in the transition to flying life-habits is diametrically opposed to the explanation assumed for many other phenomena in metamorphosis, viz. that the manifestation of new characteristics is gradually removed to ever younger instars. In my opinion the former supposition is as well justified as the latter. When for instance WEISMANN (rightly I think) assumes that changes in colour-markings of certain caterpillars, becoming visible at their last ecdysis only, have been transferred to younger stages in species near akin by a process of precession of development, the opposite course of events may also be considered possible, viz. that a colour-pattern of the wings, which originally came into existence together with the wings themselves, now

only appears a long time after the stage in which the rudiments of the wings first become visible.

Now what is true for the colour-pattern, may as well be applied to the wings themselves.

I do not intend to enter into these considerations more profoundly, as it is irrelevant for the solution of the question, whether or no the colour-pattern on the wing-sheaths of Rhopaloceran pupae possesses phylogenetic significance. • On the contrary it seems to me that in this way the question is made unnecessarily intricate. For the difference between the Lepidopterous pupa and the imago emerging from it, as well as between this pupa and the last instar but one in Hemimetabola, only consists in the limited mobility and the temporary suspension of food-supply and excretion in the pupa. In my opinion there can be no doubt that it has lost these functions, and that this loss happened gradually. For we are justified in considering the sculptured and movable pupae of primitive Lepidoptera as more original forms than the mummie-pupae, which are hardly mobile. Why then should not absence of colour and of markings be the consequence of a gradual regression of these characteristics?

Of course this explanation may be as well applied to Neuroptera as to Lepidoptera; DE MEYERE himself concedes that the pupae of Neuroptera "mostly live hidden in the earth or in cocoons, and that their chitinous envelope is thin *and only poorly coloured*". (The italics are mine).

The causes for the regression of existing colour-patterns — viz. darkness and absence of sharp-sighted enemies — which obtain all over the animal kingdom — may therefore have exerted their influence on Neuroptera. But this need not involve that the primitive Neuropterous ancestors of recent Lepidoptera already had concealed and immovable pupae. In any case those ancestors had to pass through a long range of thorough transformations, during which especially the youngest larval instars deviated ever more from the original type of the Insect, and in so doing came to differ from the last instar as well as from the last but one.

Those two stages on the contrary remained alike in all important points, though they came to differ from each other in minor accessory characters, which for the pupae chiefly consisted in the loss of mobility, with all its consequences. But apart from this immobilisation it retained the old primordial characters without or with only small modifications, and where a change still occurred, this depended more on katabolic phenomena, e.g. partial or total extinction of colour-markings, than on progressive alterations.

Therefore I think that we need no more ascribe a secondary character to the pupal stage of Lepidoptera, than we should be inclined to do so to the larval or nymphal instar of Hemi- or Ametabola. A grasshopper during the succession of its moults, passes through a series of successive stages of colour-pattern as well as a moth. The idea that the last stage but one of this series bears a different character from the preceding instars or the following ultimate stage, would never occur to us. Neither is this supposition necessary or useful for the understanding of the Lepidopterous design. That the latter is secondarily modified, is beyond doubt, it has been changed in all stages, but precisely in the pupal stage less so than in the preceding larval instar or the succeeding imaginal state, as SCHIERBEEK has shown by comparing the pupal design with that of the caterpillar in its first instar.

As to the colour-pattern of the pupa, the same considerations can be applied to it as to so many of its further properties. POULTON e.g. has pointed out, that in the pupae of those butterflies, whose forewings show a denticulated outer margin, the wing sheaths do not stop at that broken line, yet clearly marked out on its surface, but continue for a short bit and then end in an unbroken front line. He rightly takes this feature as an indication, that the ancestors of those butterflies at one time possessed normally rounded wings. In the same way he was able to show, that in those moths whose females have only vestigial wing-rudiments (the wings of the male sex being well developed) the female pupae differ much less from the male ones, because their wing-sheaths are only a little bit shorter than those of the males.

Likewise the difference between the sheaths for harbouring the filiform antennae of the females and those for the pectinate ones of the males was found to be smaller than that between these antennae themselves.

Would not all these features be caused by a recapitulation of their phylogeny, by the preservation during the subimaginal stage of former conditions which have lost their original meaning.

On this topic DE MEYERE makes the following remark: "It is difficult to explain the presence of this line" (viz. POULTON's mark) "already on the young pupal wing, otherwise than by anticipation of hereditary tendencies. Anyhow a sufficient number of instances can be adduced of cases in which features of different stages are transferred to the pupa in both directions, as well from the imago as from the larva To this same influence of precocious entrance into activity might also be ascribed the fact, that certain

markings of the imaginal wing are already visible on the pupa, e.g. the submarginal spots of *Vanessidae*. Especially when, as VAN BEMMELÉN has pointed out, the imaginal wing-pattern, during the beginning of its ontogenetic development, at first shows reminiscences of older more generalised types, we can understand, that the pattern of the wing-sheaths precisely reproduces these stages, without our being obliged to assume that the imago received its colour-markings from the pupa, and that the latter once moved about on wings ornamented in the same style''.

Referring to these considerations of DE MEYERE I should like to remark, that I do not in the least suppose the imago to have drawn on the pupa for its colour-pattern, as may clearly be seen from the inferences on p. 358 of my paper: On the phylogenetic significance of the wing-markings of *Rhopalocera*, (Transact. 2^d Entom. Congress, Oxford 1912), in which I point out the facts, that: 1. only the external surface of the wing-sheaths, harbouring the developing primaries, wear colour-markings, in contrast to that of the secondaries hidden beneath it, while of course both pairs of the imaginal wings develop a colour-pattern on both their surfaces; and 2. that the primordial or vanishing pattern on these imaginal wings is still more primitive and therefore phylogenetically older than the colour-pattern on the pupal sheath, so that there is as little reason to suppose that the latter received its pattern from the young imaginal wing hidden in its interior, as to make the opposite supposition.

The transference of imaginal features to younger instars seems probable to me also, as may be seen from the foregoing remarks. When however DE MEYERE calls this transference anticipated entrance into activity, he must have in view the activation of latent hereditary factors, and so must admit the presence of those factors in the genetics of the species. They therefore are connected with former periods of phylogenetic development, or in other words: the colour-pattern of the pupal sheaths must once have ornamented the wings of an insect flying about (or at least walking about) with them. Whether this insect was the imago or the subimago, is a question for itself, but in any case DE MEYERE's expression about "anticipated activation" includes the inference, that he also considers the pupal colour-markings as a recapitulation of a phylogenetically older stage.

Trying to enter into his ideas, I suppose them to have taken the following course: The imaginal instar of *Lepidoptera* was of old preceded by an uncoloured pupal stage. In the ancestry of the recent butterflies the peculiar habit was acquired, that their pupae no longer lived in

hidden localities, and therefore came in need of protection by mimicking- or by warning-colours. They provided for this need by means of anticipated activation, viz. by transferring the then existing pattern of their forewings to the external surface of the pupal wing-sheaths.

This pattern persisted on the pupa, even after the wings of the imago had acquired the new pattern, such as is found on them to day, by the further modification of the old one.

Even if this view of the course of phylogenetic development should prove right, which I consider rather improbable, it would not diminish in any way the phylogenetic significance of the pupal pattern, and so there would be no need to consider this pattern as wholly secondary and therefore destitute of all importance for the phylogeny of Lepidoptera. For this it would seem, is what DE MEYERE means by his words mentioned in the beginning of this paper: which fully cited run as follows:

“When precisely in the free-living pupae of the butterflies we find special colour-markings, I would consider this as a wholly secondary feature, the body having first acquired certain pigment-spots, to which sympathetic markings of the wingsheaths afterwards were added. That the latter show a certain connection with the veinal system, cannot astonish us, when we take into consideration the special importance of the veins as respiratory and circulatory vessels”.

Against this view I wish fully to maintain my own, viz. that the colour-markings of the butterfly-pupae — those on the body as well as those on the wing-sheaths — should be considered as an original pattern, the whole-colour of white, yellow, brown or black pupae of most moths resulting from the loss of this primitive design.

Regarding in particular the harmony between abdomen and wings, in colour-hues as well as in design, we may remark that such a similarity is a generally occurring feature, not only with pupae but even and in a higher degree with imagines. Without doubt this harmony will often root in a secondary modification of shades and markings, of the abdomen as well as the wings, which we may ascribe to sympathetic correlation, but this need not oblige us to doubt that both patterns result from a primitive one, or to abstain from searching after the vestiges of this primitive pattern on both those regions of the body.

What is true for the imagines, is certainly right for the pupae, even in a higher degree; remnants of the original design may be more probably expected on them and be found there in a more complete state, because the imagines are exposed to greater versabi-

lity of life-conditions and external influences, even more so than the caterpillars, their habits of moving about and resting, of nourishing and propagating being more varied.

Both caterpillars and imagines in these respects surpass the nearly immovable and lethargic pupae.

DE MEYERE'S views on this topic seem to be the cause, that while attaching great importance to the differences between the pattern on the pupal wing-sheaths of nearly related forms, such as *Euchloe cardamines*, *Pieris brassicae*, *Aporia crataegi*, he only pays very slight attention to the facts pointed out by me, viz. the great similarity between the pupal designs in several families of Rhopalocera e. g. Papilionids, Pierids and Nymphalids, a similarity not only far exceeding the resemblance between the wing-patterns of the imagines that emerge from those pupae, but also rooting in the nearer connections of this pupal pattern with the primordial and ephemerid design, which appears on the developing wings during the course of the pupal life, and only gives place to the conclusive imaginal pattern in the very last days before the emergence of the imago.

These vestigial markings on the rudiments of the wings hidden in the pupal sheaths, moreover prove to us that a primordial pattern may easily continue its existence in concealment; therefore such notions as "sympathetic colouration" or "influence of illumination and surroundings" need not be invoked in order to explain the manifestation of such a pattern.

Though the absence of markings may, in all probability, be connected with concealed life-habits and with absence of light, it would not do to consider these influences as the direct and unavoidable causes of the deterioration of the pattern. For the pattern is evidently able also to persist hidden under the pupal sheath, though in some forms it is retained much clearer and more complete than in others, without our being able to find an explanation for this difference.

Now what holds good for the wings inside the pupal sheaths, will probably also apply to those sheaths themselves. Taking this inference for granted, we might expect, that also in some of those Lepidoptera, whose pupae conceal themselves in hidden spots, the original colour pattern, on the body as well as on the wings, might have been more or less preserved.

This turns out to be really the case, as I found when studying the pupae of Chaerocampinae amongst Sphingidae, and of several genera of Geometridae. In contrast with the majority of the genera belonging to these families, whose pupae are black, brown, yellow

or white all over, the genera in question show a well marked and regular design of black markings on a light background. Yet the majority of these pupae certainly live under nearly similar circumstances as those of their relations, i. e. concealed in the earth, in cocoons or between leaves.

It is worth remarking that precisely the Chaerocampinae do not hide in the earth for the object of pupation, as many other Sphingidae do, but remain on the surface and there construct a coarse cocoon of small lumps of earth glued together with threads.

In the same way many Geometridae do not pupate inside the earth, but above it; their tissue often being so loose, that the pupa may be seen inside. I suppose that this may be the cause of the colour-markings on these pupae persisting, whereas those on their near allies have disappeared by obliteration in consequence of total darkness.

Yet the Chaerocampa-pupae in so far undoubtedly show the influence of their concealed habitat, as their markings not only are variable in the highest degree, but also show a marked tendency to obliteration. In this respect they agree with the primordial design on the imaginal wings inside the pupal sheath, and also with the maculated pattern of those butterfly-pupae, in which the original colour-mosaic is replaced by a sympathetic general hue, e.g. the uniformly green pupae of *Pieris napi*, on which the identical spots as on *P. brassicae*, may easily be detected though much smaller and less sharp than on the latter (comp. VAN BEMMELLEN, Phylogenetische Bedeutung der Puppen-Zeichnung, and SCHIERBEEK: The significance of the setal pattern in caterpillars and its phylogeny).

Therefore though the colour-design of the Chaerocampa-pupae shows deep traces of obliteration, it nevertheless is clear, that this design is founded on the same groundplan as that of butterflies. In my just-mentioned paper I have proposed a system of names (comp. fig. 6 on p. 115), according to which seven chief ranges of spots might be distinguished, called by me the dorsal, dorsolateral, epistigmal, stigmal, hypostigmal, ventrolateral and ventral rows of spots. In his essay Dr. SCHIERBEEK has pointed out, that the names of W. MÜLLER and WEISMANN, who use the expressions supra- and infrastigmal, have priority.

These rows of spots may all be met again on the pupae of sundry species of *Chaerocampa* as well as on those of *Deilephila* (e. g. *euphorbia* and *elpenor*) in various degrees of clearness and completeness.

No less striking than this correspondence in colour-design between

Sphingidial and Rhopaloceran pupae, is the connection between the markings on the pupae of the Sphinges and on their caterpillars and imagines respectively. Among the material at my disposal I found this similarity most distinctly marked in *Deilephila celerio*, as far as general completeness goes, though for certain details or on special parts of the body, other related forms sometimes showed the similarity still better and more complete, or in a more original form, as I hope to point out in a following communication;

Though I still lacked the occasion to extend my investigations to living caterpillars in their different instars, or to the development of the pupal skin beneath the last larval coat, or the imaginal epidermis inside the pupa, I do not doubt a moment but these transgressive stages will strengthen my conclusions as to the comparability of larval, nymphal and imaginal colour-design, viz. that all three are simply modifications of one and the same ground-plan, which manifests itself clearest in the pupa.

Groningen, April 1918.