

Survey of the Crystallonomical Relations between the Derivatives of *p*-Toluene-sulpho-amide
here investigated.

Name of the Compound:	Melting-point:	Symmetry:	Axial ratio:	Spec. Volume:	Topical parameters:
<i>p</i> -Toluene-sulpho-amide	137° 5 C.	Mon. prism.	1,2016 : 1 : 0,9364 $\beta = 87^{\circ}29'$	133,99	5,5537 : 4,5194 : 5,3383
Nitro- <i>p</i> -toluene-sulpho-amide	141°	Mon. prism. (pseu. o-rhomb.)	1, 2289 : 1 : 1,1812 $\beta = 90^{\circ}$	138,06	3,8442 : 3,7113 : 9,6770
<i>p</i> -Toluene-sulpho-methylamide	76°	Rhomb. bipy.	1,0358 : 1 : 2,6074	154,21	7,5664 : 7,1910 : 2,8390
Nitro- <i>p</i> -toluene-sulpho-methylamide	91°	Mon. prism.	1,0522 : 1 : 0,3948 $\beta = 86^{\circ}40\frac{1}{2}'$	165,06	7,5309 : 5,7009 : 3,9291
<i>p</i> -Toluene-sulpho-methylnitramide	60°	Mon. prism.	1,3210 : 1 : 0,6892 $\beta = 78^{\circ}6'$	152,26	4,6805 : 8,4202 : 3,4825
<i>p</i> -Toluene-sulpho-ethylamide	64°	Tricl. (pedial)	0,6481 : 1 : 0,4136 $\alpha = 77^{\circ}39'$; $\beta = 88^{\circ}6'$; $\gamma = 102^{\circ}55'$	184,55	6,6611 : 6,5633 : 4,4381
<i>p</i> -Toluene-sulpho-diethylamide	59°	Mon. prism.	1,0149 : 1 : 0,6762 $\beta = 72^{\circ}1'$	168,27	5,4115 : 5,3169 : 5,8513
<i>p</i> -Toluene-sulpho-ethylnitramide	69°	Mon. prism.	1,0178 : 1 : 1,1005 $\beta = 88^{\circ}11'$	156,91	3,4652 : 7,2001 : 6,3119
Nitro- <i>p</i> -Toluene-sulpho-ethylnitramide	76°	Mon. (sfenoid.)	0,4812 : 1 : 0,8766 $\beta = 85^{\circ}5'$	198,78	5,9793 : 6,1150 : 5,4981
<i>p</i> -Toluene-sulpho-benzylamide	113°	Tricl. pinac.	0,9778 : 1 : 0,8991 $\alpha = 83^{\circ}24\frac{1}{2}'$; $\beta = 91^{\circ}33'$; $\gamma = 95^{\circ}26'$	229,54	8,6739 : 4,7934 : 6,2983
Nitro- <i>p</i> -toluene-sulpho-benzylnitramide	153°	Tricl. pinac.	1,8095 : 1 : 1,3139 $\alpha = 100^{\circ}50'$; $\beta = 104^{\circ}43'$; $\gamma = 65^{\circ}33'$	186,57	6,5029 : 8,7005 : 3,2976
<i>p</i> -Toluene-sulpho-piperidide	98°	Rhomb. bipy.	0,7474 : 1 : 0,3790	205,20	4,2031 : 5,6295 : 8,8455
Nitro- <i>p</i> -toluene-sulpho-piperidide	108°	Mon. prism.	0,7466 : 1 : 1,5713 $\beta = 78^{\circ}39'$		

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Zoology. "The colour-markings on the body of *Lepidoptera*, compared to those of their larvae and pupae, and to those of their wings". By Prof. J. F. VAN BEMMELN.

(Communicated at the meeting of January 31, 1920).

In former communications I have expressed my conviction, that originally an intimate connection must have existed between the colour-markings of caterpillar, pupa and butterfly of the same species, all three being only varieties of one and the same archaic form. Consequently the few cases, in which this connection is evident at first sight, should not be considered as mere casualties, but as resulting from the preservation of the primitive condition. SCHIERBEEK, who chiefly studied the setal pattern of the youngest instars of caterpillars, but also gave his attention to the colour-markings of a few older caterpillars, and to pupae, has fully corroborated my views. DE MEYERE on the contrary, in his paper: *Zur Zeichnung des Insecten-im besondern des Dipteren- und Lepidopterenflügels*, 1916, has expressed his doubts about them, where he says on p. 131: "In my opinion the striking difference between the pupal- and the imaginal markings precisely shows that they have had an independent origin, and have followed different ways: — just as we found it in nearly related *Diptera*, we here see it in different stages of the same animal".

And further on:

"According to my view the colour-markings of the pupa of diurnal *Lepidoptera* are as much of recent origin as their frequently grotesque shape and their very varying mode of fixation. The same might apply to pupal markings in comparison to those of caterpillars".

In his second paper: *Zur Evolution der Zeichnung bei den holometabolen Insecten*, he writes on p. 70:

"I consider the striking colour-markings of many butterfly-pupae as a secondary feature in these organisms, exposed to light as they are. In a similar manner the pupa of *Abraaxas grossulariata*, which settles unhidden in shrubs, shows special coloration. VAN BEMMELN's assertion, that this Geometrid should show a primitive coloration in all instars, does not seem right to me, at least in regard to the pupa The pupa of *Abr. sylvata*, which hibernates in the earth, is quite dark; without doubt in this case, the older condition. The real primitive condition I believe to occur in the light-brown

pupae of many Micro's, of Hepialids, Limacodids etc., all these being very like the pupae of Neuroptera".

As I already pointed out in my paper on the primary character of the Pupal pattern in Butterflies (Proc. K. Akademie van Wetenschappen 1918) I feel justified in fully maintaining my views.

I now wish to discuss somewhat in detail, a few examples of similarity between larva, pupa and imago, chosen from the family of Sphingids. It is true that up till now I have not been able to investigate the subject in full, as I have not yet got acquainted with the younger larval instars by personal inspection, nor found occasion to study the development of the colour-pattern inside the pupal sheath. The comparison of the markings in some nearly-interrelated species of caterpillars in a full-grown state, as well amongst themselves as with those of their imagines, and in a few cases also with marked pupae, gives us such a number of striking proofs of original unity, that I consider my assertion satisfactorily backed by evidence. I therefore believe it worth-while to direct the attention of entomologists to this highly promising subject, especially so, because a complete insight into the course of evolution of the larval, nymphal and imaginal colour-patterns of a tolerably vast number of species can only be obtained by cooperation of a great many competent investigators.

From times remote the wing-markings of butterflies have attracted the curiosity and admiration of men, but to those of the body proper only in exceptional cases a little attention has been given, and then still from a purely descriptive point of view. Intercomparison of the colour-markings on the bodies of related species, or investigation of the similarity between the design on the body and that on the wings has hardly ever been tried; only when a striking resemblance between the two latter exists, is this sometimes made mention of, but only as a casual remark.

Yet it is evident, that when comparing the imago with its caterpillar, only the markings of the body need be minded, and that the same applies to the pupa, though in a minor degree, as in the latter only the upperside of the forewing is exposed to view, while on the contrary part of the lateral body-wall is hidden beneath the wing-sheath.

When moreover we wish to study the connections between the markings on the wings and those on the body, it seems desirable first to realise the exact nature of the wings. Now these organs may be considered as lateral folds of the dorsal skin of the meso- and metathorax, near to and dorsally of the line of stigmata (though these openings are obliterated in the said segments of the thorax). Consequently each wing consists of a dorsal and a ventral lamella of

the skin, which along the wing-border fold over into each other. When we imagine this fold to become repressed up to the first initial rudiment of its evolution, then these lamellae do not extend horizontally along parallel planes in contact with each other, but quite the contrary lie in one and the same dorsoventral plane. When in applying this mode of representation of the wing we look at it from the side, it is seen projected on the lateral body-wall, and so each wing can be drawn as a sexangle, which by its horizontal diagonal is divided into a dorsal half (the upper wing-surface) and a ventral one (the underside of the wing): the diagonal itself representing the wing-border. That by this projection-method the wing-field appears extremely small in relation to the dimensions of the body, need not according to my view be considered as a real objection against it. For the relation in size between wings and body in different species of Lepidoptera varies between very wide limits, and in the females provided with rudimentary wings of sundry species it even approaches the schematic condition described. Likewise during the pupal stage of almost all kinds of Lepidoptera the wings are far smaller than after the emersion from the nymphal sheath.

This projection of both wing-surfaces upon the dorso-ventral plane sharply draws our attention to the fact that markings, which on the wall of the body stretch in an oro-aboral direction, will run in a so-called transversal one over the wing-surface, i. e. from the anterior towards the posterior wing-border. The dorso-ventral components of the pattern on the contrary will traverse the wing-field from root to external margin (commonly called longitudinally). In the same way this method can give support to the belief, that the pattern of the upper surface need not originally have been identical with that of the underside, as they correspond to different, though neighbouring areas of the sidewall of the body.

Finally this way of representing the wings as projected on the body highly facilitates and accentuates the comparison with the caterpillar. To get a pure comparison with the pupa however, we are obliged somewhat to modify the position and the size of the sheath of the forewing, which involves the formation of an empty space towards the side of the abdomen, corresponding to the place where the hind-wing would have been situated, when this were visible on the pupa.

In order to insert the real wing-pattern into these schematic sexangles, we have to project it upon them. To do this, we must turn the wing obliquely up- or downwards and draw a contracted image of its colour-pattern on the perpendicular plane of projection.

Moreover it is desirable to apply this same method of projection to the dorsal and ventral body-wall, in such a sense that the circumference of the figure no longer corresponds to that of the sideview of the animal, but roughly forms a trapezium, the upper- and under-side of which represent the median dorsal and ventral lines, or better still, stretch a little over them. This can also be expressed in such a way, that the body becomes compressed from left to right, thereby growing higher in the dorsoventral direction, a condition so often shown in reality by squeezed specimens. As to the position of the wing-sexangles in regard to each other, I am of opinion that they should be placed in one and the same horizontal body-axis, the one behind the other, instead of the anterior margin of the hindwing passing beneath the posterior one of the forewing. In size the two wings may be represented alike. The arguments for both these assumptions can be found in the wings of Hepialids.

Consecutively the following points should be attended to in the investigation:

- a. comparison of the markings of the thoracal with those of the abdominal rings in one and the same individual, therefore in the caterpillar with its different instars, in the pupa, and in the imago.
- b. comparison of the colour-pattern of all these stages, to each other in the same species.
- c. comparison of kindred species in their successive stages with each other.

For each of these comparisons an example may be given.

Of the few Sphingid-caterpillars which were at my disposition, I choose the fullgrown larva of *Protoparce convolvuli* (scil. the brown variety) as a fit object for comparison of thoracal with abdominal markings. For in this species the relation of the one to the other can be very clearly observed, and in doing so, we are impressed by the fact that the first seem to bear a more primitive character than the second. For on the thorax the obliquely ascending lateral bars, which are so characteristic of the abdominal segments of these as of so many other Sphingid caterpillars, are absent. The pattern is restricted to longitudinal light and dark stripes, which in their turn are evidently composed of rows of spots, whose number corresponds to that of the annuli or secondary rings, which enter into the composition of each body-segment of the caterpillar. The number of these annuli is constant, eight for each segment of the abdomen, except the posterior two; it is likewise diminished in the thoracal ones, probably an effect of reduction. On each annulus one row of light spots on a dark ground is seen. The relative size of the single

spots determines the impression they call forth, either of a light or of a dark party of the caterpillar-skin. While light spots on the same level on successive annuli arrange themselves to light longitudinal stripes, small spots on the contrary appear as light specks in a dark band. Here and there these specks totally vanish, a larger black spot being the result. So the prothorax shows no other ornamentation than a pair of big epistigmal dark blotches on its flanks, passing in a caudal direction into the dark longitudinal strokes, which on the abdominal segments periodically become transected by the oblique light stripes. On meso- and metathorax a light brownish-yellow median dorsal stripe is present, flanked at some distance by light subdorsal stripes, separated from the firstnamed by dark bands, which in the anterior part of each segment bear the character of dark spots.

Beneath the line of the stigmata runs a very broad light streak, over the roots of the legs two dark longitudinal lines are seen.

All these markings are found again on the abdominal segments, but in a modified, more complicated condition. The dorsal stripe passes uninterruptedly from thorax to abdomen in the form of a light band, slightly contracting in the middle of each segment, while at its anterior margin a pair of yellowish-white spots, separated by a small dark stripe, contribute to render the first annulus of each abdominal segment more conspicuous. But in the first place this effect is reached by the two sharply drawn brownish-black spots at the lateral side of the just-mentioned light dorsal maculae, and by the clear white specks, which in their turn flank the outer side of these maculae.

This series of alternately light and dark spots on the first annulus evidently only consists of nothing more than highly conspicuous links in the prolongation of the above mentioned three light and two dark lines that run over the dorsal side of the thoracal segment. It is therefore in harmony with this fact, when we remark that from each of the black blocks a dark streak runs on in a caudal direction. These streaks converge towards the centre of the segment, in harmony with the median light dorsal streak, which narrows in the middle of each abdominal ring, while towards the back end of the segment the streaks again diverge. Consequently the dorsal stria broadens towards the latter margin and so forms a triangular area, which somehow assumes the character of an independent spot; this aspect being heightened by the repetition, in the centre of the segment, of the small black stripe in the middle line on the first annulus.

Looking from the lateral side, the similarity between thoracal and abdominal designs likewise strikes us, but at the same time we remark the deviation of the latter from the original condition, in

consequence of the differentiation of the oblique light stripes which ascend in a dorso-caudal direction, and are accompanied along their dorsal border by an obscuration of the brown-black ground-colour (called "dunkle Grundierung" by v. Voss). At their posterior top these oblique light stripes exactly pass into the above-mentioned white subdorsal spots, in the same way as their accompanying dark seams join the black specks, which themselves run on into the dark subdorsal lines. A similar broadening and obscuration of the seam, as is caused by these specks at the dorsal end of the oblique stripes, is also found at their ventral beginning, on the level of the stigma. The latter however is situated at the back side of the light oblique stria (on the suture between the 3 and 4 annulus), while the mentioned dark spot lies before it on the 2 annulus. Still further forward to the front side, the corresponding part of the first annulus also bears a pair of dark maculae (praestigmal spots). The stigma itself is likewise coloured dark. In advance of the stigma the dark diagonal stria is still continued in a ventral direction over the posterior four annuli of the foregoing segment, and reaches the ventral border of the broad light substigmal band, where it joins the horizontal undulating line over the base of the false legs.

Now in this brown variety of *convolvuli* we see at once that all these spots and stripes are nothing else but more or less differentiated parts of the general ground-pattern, which exclusively consists of rows of light maculae on a dark ground, keeping rigorously to the annuli, and therefore repeated eight times on the succeeding abdominal segments. In each row the number of maculae is large, yet tolerably constant, viz. ± 13 at either side of the median line.

The above described black spots are formed by the blending of dark stripes separating the white specks, the light blotches on the contrary by the obliteration of one or more of these stripes.

Likewise the light diagonal stripes are built up by an obliquely rising series of eight light maculae that have increased a little in size, the dark seam in the same way by a similar gradation of black cubes, lying dorsally to these light maculae.

Comparing the brown with the green variety, we remark that the latter has got nothing left of the entire ground-pattern but the larger dark maculae: the subdorsal, the epistigmal, the prostigmal, the stigmal and the hypostigmal or the basal spot. Of these the epistigmal spot still betrays its original character as a part of the dark seam along the diagonal stria by its obliquely extended shape in a dorso-caudal direction, pointing so to say to the subdorsal stripe of the following segment.

On the metathorax of the green variety the subdorsal spots are present in double number, on the metathorax in single.

Comparing the larval design to that of the imago, we may here remark in parentheses, that the last-mentioned pair of spots also occurs on the caterpillar of *atropos* and here maintains itself as the eye-spots of the cranium-image.

The collection KALLENBACH also contains a halfgrown *convolvuli*-caterpillar, I therefore found occasion to compare this with the fullgrown larva, and thus could convince myself that the light subdorsal maculae of the latter really are the remnants of a complete subdorsal line, originally stretching over the whole series of the body-segments, in the same way as the substigmal line. On the abdominal segments however it is periodically broken by the diagonal striae which, though rather inconspicuous, are yet present in complete order, and which, before each stigma, meet the segments of the substigmal line, thereby forming a triangular spot on each body-ring. But the chief difference between this halfgrown caterpillar and the fullgrown one is its uniform dark ground-colour, sharply contrasting with numerous small white oval knobs, which stand arranged in several rows on the eight annuli. On the above-mentioned light longitudinal lines these knobs occur in the same way. They do not make the impression of standing in any relation either to the dark or to the light specks, their own hue in fact is a much clearer white than that of the latter. So we can only suppose, that at the last moult they disappear, to be replaced by the (tolerably regular) white spots in the dark ground-colour.

When we pass from the caterpillar of *convolvuli* to that of *atropos* and *ligustri*, the design of these latter two is seen to correspond to that of the first in all such instances, as can be considered as secondary modifications of the original pattern; those parts of it on the contrary, which in *convolvuli* are found in the least modified condition, having nearly vanished in the other two species. The same may be said of the thorax: here the process has led to total absence of pattern in *atropos* and *ligustri*. Upon the abdominal segments on the contrary the pattern is the same for all three, only differing in shades and in completeness.

These facts undoubtedly offer new and valuable arguments for the supposition, that the absence of pattern is a consequence of obliteration; the two latter species therefore having suffered stronger regression from the original condition than *convolvuli*.

Still in another instance the lastnamed species seems to show the more primitive conditions, viz. in the simple and few colours that

enter into the composition of the pattern: darkbrown and diluted yellow. It is true that these colours only maintain themselves in the older instars of the larval period, as originally the caterpillar is green. So when we should ascribe a general applicability to the rule that the colours and markings of the younger stages invariably represent more original conditions than those of the later, we should be obliged to suppose that the brown colour had arisen from the green one. But though this rule can be applied in many cases, it by no means may be considered as of universal validity. Especially in insects I am of opinion that everywhere the green colour is a secondary modification of other shades, which lie farther to the red side of the spectrum, as I have already tried to demonstrate in my paper on the genus *Charagia* among *Hepialids*.

In *convolvuli* therefore the change from green to brown should be considered as a reversion to more primitive conditions, and in connection with this supposition we might regard the green colour in *ligustri*, and to a certain extent also in *atropos*, as due to secondary modification¹⁾. Possibly this change in the general shade might be brought in connection with the reduction of the original design, which on the thorax has led to complete, on the abdomen to partial obliteration, and moreover on the latter has called forth a greater contrast between the uniformised green ground-colour and the very obvious pink and white oblique striae.

As a hint that in *convolvuli* the brown caterpillar has best retained the original character, we may also regard, that in this species the connection of the markings with the everywhere occurring subdivision of the body-segments in a series of eight annuli or subsegments is most conspicuous. But likewise in the other two species it is obvious that the diagonal striae (pink and white in *ligustri*, pink and yellow in *atropos*) are composed of a step-like series of dark and light blocks of colour. With regard to this feature, those of the firstmentioned species strike us by the peculiarity, that in the forward prolongation of the diagonal striae on the foregoing segment a row of three or four white specks occurs, growing smaller from behind forward. In this anterior prolongation of the white striae the blending of the specks, which enter into their composition, has not yet taken place.

In the green caterpillar of *atropos* another proof is seen for the assertion, that more extensive striae, bands and fields of colour are the result of the blending of smaller spots arranged in transverse rows. For

¹⁾ This species also possesses a brown variety of the caterpillar, and this, as well as that of *convolvuli*, shows a more complete and primitive pattern than the green one.

on the bluish dorsal stripe as well as on the neighbouring yellow subdorsal bands and the pink-red oblique lateral bands, we find groups of knobs, which evidently are regularly arranged on both sides of the median line, in eight transverse rows, which correspond to the annuli composing each segment, the number of the wharts in the blue diminishing from before backwards in the ratio of three to two to one. Each knob carries a hair, or at least was originally provided with one. On the pink bands the knobs have the same hue as the band itself, only a little deeper, in the yellow and the blue on the contrary they retain that same pink colour of their own. On the anterior row of each segment, where the number of wharts in the blue reaches its maximum (3 or 4 at each side of the median line) the wine-red colour even extends around the two lateral tubercles, and embraces them in one larger deep-red blotch. Surveying the whole of the segments, these blotches are seen arranged to both sides of the median line in a series marking the subdorsal line; this series can be retraced in *convolvuli*, in the form of the rows of dark subdorsal spots described before, which rows are in immediate contact with similar ranges of clear yellow-white maculae, nearer to the dorsal line, the latter itself being marked by dark stripes (3, one behind the other, on each segment).

When now we pass to the survey of the body-markings of the imagines and begin with the abdominal segments of *convolvuli*, we here again meet the dorsal line as a series of little black stripes. To both sides of this the subdorsal design is arranged as a sequence of grey areas touching the dorso-lateral colour-markings with a special convexly-curved borderline. These fields themselves are composed on each abdominal ring of three transverse bands: a narrow anterior one of white, and two much broader ones behind, the first pink, the second jet-black. This set of three transverse bands is repeated seven times: at the end comes one segment with only a black dorsal stripe. The ventral border of this lateral pattern forms an almost straight line, situated at a certain distance above the row of stigmata. The intervening epistigmal seam is coloured less conspicuously in the same way as the entire hypostigmal ventral surface; yet it is possible to distinguish darker sets of hairbundles, which associate with the red and black bands, and a row of white bushes of hair stretching right above the stigmata.

Though as mentioned, the ventral side shows no vividly coloured pattern, this uniformity of hue is precisely the cause, that a set of two dark spots in the ventral middleline, at the front-border of the fourth and the fifth abdominal segment, is highly conspicuous.

In my opinion the transverse markings of the dorsolateral fields might be ascribed to the original distribution of the colour in dorso-ventral bars, corresponding to the eight annuli which enter into the composition of each segment; probably the white represents the first annulus, the pink area the following four, the black the posterior three, but in *convolvuli* the limits of the single rings are indistinct. As we shall see, this division can really be traced in imagines of other Sphingids.

Now comparing this pattern of the abdomen to that of the thorax, we remark that the grey ground-colour along the dorsal side of the latter, provided with three darker longitudinal striae on both sides of the middle-line, evidently may be considered as a broadening of the dorsal markings of the abdomen. Over the root of the wings runs a greyish-white streak of long, soft hairs, forming a continuation of the white transversal markings of the abdominal segments, especially of their dorsal part, which on the second segment already has the shape of an isolated round white blotch. This light stripe over the wing-root (epipterygial stripe) should probably not be considered the homologon of the white subdorsal line on the thorax of the caterpillar.

In the third place an evident connection exists between the markings on the upperside of the hindwing and those on the dorsal side of the body, as well of the thorax as of the abdomen. The said wing-design consists of dark spots arranged in bands on a lighter ground. These bands apparently stand perpendicularly to the longitudinal axis of the body, thereby agreeing in position with the anterior three black transversal rings on the abdomen. As a matter of fact however they are not transverse but longitudinal bands, because they run from the anterior towards the posterior border of the wing, the apparent transverse position only being a consequence of the rounding off and reduction of the hindwings, which in Sphingids has taken place in an extreme degree.

When as described before, the hindwings are projected upon the lateral walls of the thorax, the dark bands may be drawn on the wing-fields as *longitudinal* lines, viz: in an oro-caudal direction. In this way the similarity with the lateral design of the abdomen, which at first aspect is so striking, withdraws to the background, or, rather, is reduced to its real proportions.

Indeed, as well as the design on the annuli of the thoracal segments of the *convolvuli*-caterpillar, that on the wings is seen to consist of dorso-ventral rows of alternately dark and light spots, which are arranged in longitudinal chains, by their situation at the same level

upon the succeeding annuli. It is true that the surface of the wing is not divided into regular annuli in the same way as the body-wall, yet also its surface becomes parcelled into so-called cells by means of the venous system, this division showing a considerable amount of similarity to the first-mentioned division in annuli. One even might feel tempted to ascribe a certain importance to the fact, that in the neighbourhood of the wing-root the number of internervural cells is equivalent to that of the annuli of the larval segments, when the original number of veins in the proximal area of the wing is taken to be eight, (costa, subcosta, radius, medius, cubitus and three anals).

Comparing the body-design of the *convolvuli*-imago to that of the corresponding stages of *ligustri* and *atropos*, the similarity is obvious on first view, and not less striking than that of the wing-patterns. But entering into details, which at first sight might seem to be trifles without deeper meaning, a few curious features may be remarked, which draw the original similarity with the caterpillars into stronger evidence. So in *ligustri* the contrast between the light areas on both sides of the black median dorsal line and the enlarged dorsal tops of the black transversal bars, is sharper than in *convolvuli*, these broadened black tops, protracted as they are towards the head-side, producing the impression of a sequence of dark subdorsal spots separated by the lateral emergencies of the front-corners of the lightbrown subdorsal fields, in a higher degree than is the case in the lastnamed species.

Likewise in *ligustri* the white lateral transversal stripes along the frontborder of the segments are lacking, or to express it more correctly, the white is replaced by black, which coalesces with that along the back-border of the foregoing segment, the black between the first and the second abdominal segment being restricted to a subdorsal blotch. Moreover the ventral ends of the black and of the red transversal bands are obliquely truncated, which calls forth the impression of a zig-zag-line, running at a certain distance above the series of the stigmata, which line corresponds to the system of diagonal stripes on the abdominal segments of the caterpillar.

At the ventral side the design has remained unaltered in a much higher degree than in *convolvuli*, the dark ventral line stretching over the whole of the segments. At both sides of this line light areas are found, which at the level of the stigmata are marked off by a dark festooned line. On the thorax the resemblance with *convolvuli* is striking, and especially the light epipterygial band is drawn with peculiar sharpness.

The similarity in design between the abdominal segments and the hindwings is still more obvious than is the case with *convolvuli*,

because in *ligustri* the groundcolour of the hindwings plays into a rose-red hue, especially in the neighbourhood of the wing-root, this red even running over into the root of the forewings. The black wingbands lie more exactly in the prolongation of those of the anterior abdominal segments and show fewer traces of their origin by the coalescence of a row of intervenous spots.

All the above-mentioned resemblances are equally found in *atropos*, only the hues and the variegations being different: When we start from the abdomen, the dorsal stripe on its back corresponds to that of the caterpillar as well in the V-shape of its segments as in its blue shade. The rose-red colour of *convolvuli* and *ligustri* is replaced by stark-yellow and the dorsal borderlines between the yellow lateral areas on the abdomen and the blue dorsal patches run in the same oblique direction as the lateral sides of the V-shaped elements of the dorsal design in the caterpillar. At the ventral side of the abdomen the black design along the frontborder of the segments, at least of the anterior ones, is well developed, and shows well-marked enlargements along the hypostigmal and subventral lines, pointing to the presence of series of spots at those levels.

As well as in *ligustri* the light (in *atropos* yellow) hue of the lateral walls of the metathorax is continued not only on the hindwings, but also on the root of the forewings, though it does not reach the front-margin of these latter.

The cranial design on the dorsal side of meso- and metathorax may be easily traced back to sets of dark spots on a light ground: two pairs of these spots standing on the meta-, one on the mesothorax, just as is found in the caterpillar, and in the same way in the imagines of many other Sphingids as well as in those of other Heterocerous families. The contour of the skull-image corresponds to the dorsal or medial dark longitudinal thoracal line, which forms the borderline of the median area of the thorax, in the same way as in *convolvuli* and *ligustri*. The more ventral or lateral thoracal-line is likewise present in *atropos*, and next to it also the epipterygial light streak, though here this latter does not show the grey shade of *convolvuli* or the white of *ligustri*; but a dark bluish grey, which of course renders it much less conspicuous.

Lastly comparing the three stages of *Chaerocampa celerio*, as well with each other as with the corresponding stages of the three above-mentioned Sphingids, we meet again with all the already remarked peculiarities, but here they are in some regards more complete and better pronounced, in other points more original, in still other on the contrary more modified, either in a higher degree or in a different way.

E.g. in the fullgrown caterpillar the contrast between thorax and abdomen is of the same nature and as strikingly pronounced as in that of *convolvuli*. The dorsal stripe is only marked by a thin but sharply drawn black line, extending all along the thorax, but on the abdomen only covering the anterior three segments. The light subdorsal and epistigmal lines on the contrary are well developed on the thoracal segments, the first runs up to the big ocellus-spot on the first abdominal ring, this spot, as WEISMANN'S investigations have proved, differentiating itself in the course of development of the caterpillar from the anterior part of the subdorsal line on this segment, while at the same time the posterior part obliterates.

The second eye-spot is formed in the same way. In the specimen at my disposal this spot was much bigger and more purely circular at the left side of the body than at the right. On the latter side however the spot consisted of two parts, lying immediately behind each other, and so betrayed its real nature as a part of the subdorsal line still better than at the opposite side.

On the next abdominal segment traces of the light subdorsal line can still be detected, and likewise of dark spots immediately above it on the level of the first annulus. Above the stigmata of the abdomen dark diagonal striae run upward, bordered at their ventral side by light stripes: proving that the common motive of design of the Sphingid caterpillars is present also here. These striae and stripes, though occupying the whole length of the segments, yet figuratively speaking seem to be drawn on a back-ground of light spots and dark stripes, which themselves are strictly bound to the division of the segments into annuli.

Moreover a contrast exists between the dorsal and the ventral side. On the first we meet at every annulus with a row of small black stripes, between which the ground-colour is lighter and therefore makes the impression of clear spots separated by black lines. This part of the design shows a great similarity with the annuli-markings of the full-grown *convolvuli*-caterpillar.

At the ventral side on the contrary each annulus carries a row of white lentiform knobs, constituting the basal cushions of short setae. On the level of the epistigmal area the knobs pass into the light spots, evidently the latter occupy the same place as the former, at least the knobs diminish in size and conspicuousness towards the dorsal side. This feature therefore confirms the assertion that the colour-pattern of the fullgrown *convolvuli*-caterpillar may be derived from the condition before the last ecdysis, by supposing the knobs to fall out and to become replaced by the light spots. It also deserves

attention, that in *celerio* the knobs have maintained themselves at the ventral side of the caterpillar, in *atropos* on the contrary at the dorsal surface, while in *ligustri* they are totally absent, probably an effect of obliteration.

These rows of knobs, standing regularly arranged along the annuli, probably represent the same feature as the chagration of the larval skin, mentioned for many Sphingid-caterpillars by WEISMANN and Voss, these investigators however having paid no special attention to this feature. When studying the figures, which the latter author gives for the younger instars of the *Smerinthus*-caterpillars e.g. the yellowish-green variety of *S. ocellatus*, (fig. 22, III stage and 23, III stage), we find distinct indications of these light spots arranged in a dorso-ventral row on the annuli. Judging from older figures of *Ceratoma amyntor* and *Pogocolon nesus*, the rows of setiferous knobs here run regularly from the dorsal to the ventral side of all the segments, those of the thorax as well as those of the abdomen.

Now comparing the caterpillar of *celerio* with the body of the moth, the correspondence in design in many regards is still more striking than in the before-mentioned species of Sphingids. For on the dorsal side of the abdomen of the imago the markings consist of alternating light and dark longitudinal lines, and these lines are seen to be composed of a chain of coloured patches, which on every segment clearly show the division into annuli, just as on the body of the caterpillar. On the first and the last annulus of each segment the design is developed best: silvery-white spots in the dorsal median line and subdorsal stripes marking the anterior and the posterior border of the anterior abdominal segments. Along either side of the median line (which behind the mentioned white spot carries a series of black stripes), dark bands run in a longitudinal direction; these as well as the median stripe are prolonged over the thorax. To the lateral side of these three dark bands a silvery stripe is formed, the homologue of the subdorsal line, and over the root of the wing we again meet the light epipterygial stripe which runs on to the head above the eye, and shows a great similarity to the epistigmal stripe of the caterpillar. But on the abdominal segments we are likewise able to distinguish stigmal, hypostigmal, subventral and ventral longitudinal bands, and we also see that the epistigmal, the subdorsal and the dorsal bands are characterized by the occurrence of silvery-white bushes of hairs. Using a magnifying glass for more minute observation, each of these stripes is seen to be again composed of lighter and darker bushes and groups of specks, the whole circumference from the dorsal to the ventral median line therefore

showing no less than 27 colour-patches varying in hue. E.g. the brownish-black bands to either side of the dorsal median stripe are by no means uniformly coloured, but show a mosaic of black and light scales. These bands pass on to the thorax almost unmodified. Especially the continuation of the subdorsal stripe on the thorax is striking, as the white bushes, which characterize this stripe on the abdomen, are also seen on the thorax. The epipterygial stripe evidently represents the prolongation of the epistigmal line, this line being likewise marked by yellowish-white bushes. Behind the eye the subdorsal and the epipterygial stripe unite into one.

But traces of the diagonal stripes may, I believe, also be detected, at least in some specimens, in the shape of dark and light oblique bands on the sides of each segment, above the stigma. Those features which in *celerio* are either absent or very indistinct, are unmistakably present in other species, e.g. *alecto*. About the wing-design of *celerio* we still want to remark that the considerable difference between the upper surface of the fore- and that of the hindwing, in contrast to the nearly perfect similarity of both wings at their underside, probably points to the fact, that the upperside has become secondarily modified to an important degree. Now it is remarkable that at this side the forewings, in hues as well as in design, show greater similarity to the dorsal side of the thorax and abdomen than does the hindwing, notwithstanding the fact that on the first-named the V-diagonal design (as I have called it) is strongly expressed. Moreover this design, with regard to the direction of the diagonal-line, possesses a striking similarity to the oblique markings on the abdominal rings of the caterpillar. This similarity especially enters into evidence, when the wing is projected in the above-described way on the lateral wall of the thorax.

In conclusion I wish to say a few words about the design of the pupae, which in Sphingids, as already mentioned in a foregoing paper, has been preserved more or less, especially in the group of the Chaerocampinae. It consists of dark blotches on a lighter ground: shape and size of these blotches is rather irregular, yet it is clear that they are arranged in rows, corresponding to the dorsal, subdorsal, epistigmal, stigmal, hypostigmal, subventral and ventral lines of the caterpillars and imagines. In a few specimens, which I found occasion to investigate (amongst which was one of unknown derivation, the species therefore remaining uncertain to me) the number of these rows of spots is much higher, which leads to a striking resemblance with the design of imagines, especially *celerio*. Though I could not yet find leisure to study in details the similarity between caterpillar

and imago (eventually also pupa) of other forms than the Sphingids, I feel convinced, that it may be proved for a great many Lepidoptera, e.g. Saturnidae and many Bombycidae, and certainly also for Geometridae.

From the above mentioned observations I feel justified in making the following deductions:

The markings on the body of caterpillars, pupae and imagines follow the same rule as those on the wings of the latter. Consequently the original design is regular, simple, limited to each segment separately, complete, uniform over the whole extent of the segment, bound to the dispersal of the setae over its surface, and to the division of the latter into secondary rings or annuli. The colour, in which this pattern is executed, may differ, and is of no account as to its real character. Yet there exists a certain connection between different hues: green for instance always appearing as a secondary modification of other shades, especially brown, grey or yellow.

Modifications of the original pattern take place in a similar way and after the same rules as those on the wings. Through the accentuation of a contrast in shades between neighbouring spots, which originally were similarly coloured, a richer gamma of hues may be produced. Vertical, horizontal and oblique lines are formed by coalescence of rows of primary spots; maculae, eye-spots, bands and areas result from the accrescence of spots and (or) their blending with others in their vicinity. Finally the whole bulk of the separate spots may merge into one general shade.

Attention should also be paid to the fact, that in the same way as the front-seam of both wings is often marked in a different and stronger way than the rest of the surface (especially at the under-side), the first annulus of each segment likewise surpasses the rest of the annuli in sharpness of design and coloration.

However restricted the material for my investigations may have been, it has convinced me still more of the validity of my assumption, that a primary relation exists between the colour-design of caterpillar, pupa and imago, the pattern of the imaginal instar often showing a more primitive type than that of the fullgrown caterpillar.

The contrast between thoracal and abdominal pattern, which already in the younger instars of the caterpillar manifests itself in the different distribution of the setae (comp. J. T. OUDEMANS and A. SCHIERBEEK), maintains itself as well in the later instars by differences in colour and design, occurring in the great majority of caterpillars. An identical design on thorax and abdomen is probably the result of secondary change.

Groningen, January 1920.

Physics. — "*On Centres of Luminescence and Variations of the Gas Pressure in Spectrum Tubes at Electrical Discharges.*"

By L. HAMBURGER. (Communicated by Prof. H. A. LORENTZ).

(Communicated at the meeting of April 23, 1920).

1. *Introduction.*

Three years ago¹⁾ we published the results of some observations, in which among others the fact was stated that when discharges are sent through a spectrum tube, variations of the gas pressure may occur at the anode and the cathode.

They owe their existence to the difference in properties of positive and negative ions. As J. STARK²⁾ already observed, the difference existing between the two kinds of ions gives rise to the two following effects:

a. The appearance of phenomena connected with the electrical wind (in general the electrostriction).

b. Mass transportation by means of the electric current.

The object of this paper is among other things to examine which of these two effects, which are in connection with each other, as they both rest on the difference in properties of the ions, has a greater part in the observed variations of the gas pressure. In connection with this the centres of electro-luminescence will then be considered.

2. *Electrostriction.*

A Dutch physicist D. Bos³⁾ has already made an extensive study of this. He finds for gases such slight variations of volume, resp. of pressure, (loc. cit. p. 92 et seq.), that it is clear that with the pressure effects observed by us — to an amount of 30 % and more of the total pressure — electrostriction cannot have had an appreciable direct influence.

In the case of discharges through a spectrum tube the phenomena of the electrical wind connected with electrostriction may be considered as a consequence of the friction between the ions and the neutral gas molecules. It is clear that the electrical pressure will be the greater as the difference in properties of the positive and negative ions is greater. As we already mentioned, this electrical pressure is of an entirely different order of magnitude than the variations of the gas pressure observed by us.

¹⁾ L. HAMBURGER, Diss. Delft 1917. These Proc. **20**, 1045 (1917).

²⁾ J. STARK. BOLTZMANN-Festschrift 1904.

³⁾ Diss. Groningen 1880.