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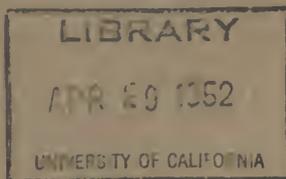
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ON THE SETAL PATTERN OF  
CATERPILLARS AND PUPAE.



A. SCHIERBEEK.



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# ON THE SETAL PATTERN OF CATERPILLARS AND PUPAE.

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PROEFSCHRIFT TER VERKRIJGING VAN DEN GRAAD  
VAN DOCTOR IN DE PLANT- EN DIERKUNDE  
AAN DE RIJKS-UNIVERSITEIT TE GRONINGEN, OP  
GEZAG VAN DEN RECTOR-MAGNIFICUS DR. C. VAN  
WISSELINGH, HOOGLEERAAR IN DE FACULTEIT DER  
WIS- EN NATUURKUNDE, TEGEN DE BEDENKINGEN  
DER FACULTEIT TE VERDEDIGEN OP ZATERDAG  
20 JANUARI 1917, DES NAMIDDAGS TE 3 UUR, DOOR  
**ABRAHAM SCHIERBEEK**, GEBOREN TE LEEUWARDEN.

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N. V. BOEKHANDEL EN DRUKKERIJ  
VOORHEEN E. J. BRILL, LEIDEN 1917.



AAN MIJNE VROUW.



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Aan het einde gekomen van de bewerking van mijn proefschrift, zie ik nog gaarne eens terug naar den 14den Augustus 1914. Midden in den pas uitgebroken wereldoorlog scheen het mij haast een bespotting om met nieuwen moed aan een mij totaal onbekend onderwerp te beginnen. Het kwam mij soms wel wat dwaas voor, om, waar tallooze, de gansche wereld beroerende problemen ook mijn aandacht bezighielden, al de energie, die niet verbruikt werd door mijn meer dan 35 lesuren per week, te besteden aan de studie van *de plaatsing der haren op de rupsen*.

Mocht ik hierdoor wel eens wat terneergedrukt worden, dan kwam te juister tijd één Uwer opwekkende brieven, Hooggeleerde VAN BEMMELEN, om mij weer met lust aan het werk te doen gaan. Nu ik mijn arbeid, naar ik hoop voorloopig, heb afgesloten, en ik de met U gevoerde correspondentie nog eens doorlees, nu wordt het mij weer duidelijk, dat veel wat ik geheel als eigen werk beschouwde, toch zijn ontstaan te danken heeft aan Uw belangstellende vragen. Ik hoop, dat Gij niet alleen als Promotor bij de bewerking mijner dissertatie, maar ook later, mij Uw welgemeende raadgevingen en hartelijke belangstelling zult blijven schenken. Voor de hulp, mij bij dit werk verleend, voor Uw uitstekende raadgevingen bij het vertalen in het Engelsch, en voor de gelegenheid, mij door U geschonken, om zelf te ondervinden „hoe wetenschap gemaakt wordt” ben ik U ten zeerste dankbaar.

Hooggeleerde BONNEMA, als gymnasiast van nauwelijks dertien jaren kwam ik reeds onder Uw leiding. De groote liefde voor de natuurlijke historie in haar geheelen omvang, die Gij bij Uw leerlingen opwekte, heeft velen ertoe gebracht om deze wetenschap tot het vak hunner keuze te maken. Waar ik nu reeds eenige jaren als leeraar Uw lessen in praktijk breng, daar streef ik ernaar het

zelfde te verkrijgen, wat Gij bereikt hebt. Ik hoop, dat Gij mij Uwe vriendschap ook verder niet zult onthouden. Het vele, dat ik U verschuldigd ben, als gymnasiast, als student en als leeraar, zal ik steeds in dankbare herinnering houden.

Hooggeleerde MOLL, ik hoop, dat Gij in dit proefschrift iets van de methodische en zuiver wetenschappelijke behandeling van een onderwerp terug moogt vinden, welke Gij steeds als eerste eisch voor degelijk en vruchtdragend onderzoek aan ons hebt voorgehouden en waarvoor Gij U zooveel moeite getroost hebt om ze Uwen leerlingen bij te brengen.

U, overige Hoogleraren der philosophische faculteit, wier colleges en practica ik heb mogen volgen, ben ik zeer erkentelijk voor alles wat ik van U heb geleerd.

Hooggeleerde HEIJMANS, KAPTEIJN en van WIJHE, veel van mijn vorming ben ik U verschuldigd. Als gast op Uw colleges heb ik veel geleerd en ik hoop, dat Gij hiervoor een woord van dank wel wilt aanvaarden.

Mevrouw KUENEN, Uw zoo welwillend aangeboden hulp bij de correctie van den Engelschen tekst, is door mij op hoogen prijs gesteld.

Uit vriendschap hebt Gij, EMIL GRUNO, de moeilijke taak op U genomen mijn studie te vertalen. Met voldoening kunt Gij op Uw arbeid terugzien en Gij weet hoe zeer ik Uw werk waardeer.

Aan mijn VROUW heb ik mijn proefschrift opgedragen. Tusschen de beslommingen van huishouding en artsen-praktijk hebt Gij tijd gevonden mij op velerlei wijzen te helpen en een gedeelte van mijn manuscript te vertalen. Ook op deze plaats past hiervoor een woord van dank.

's Gravenhage, 7 October 1916.

## CHAPTER I.

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### INTRODUCTION, MATERIAL AND METHOD.

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#### § 1. Introduction.

The well-known treatise of WEISMANN (1876) on the Sphingid-caterpillars has given rise to many recent investigations of the Lepidoptera. It very soon became evident that many important discoveries could still be made about these well-known insects, although they have been observed for centuries, even if one confines oneself to external characteristics only. The studies of WEISMANN on the seasonal dimorphism (1876), the rediscovery of RATZEBURG's observations (1840) on the external sexual characteristics of the pupae by JACKSON (1890) and POULTON (1890), the studies by POULTON on the antennae and wingsheaths of the nymphae, the enlargement of our knowledge of the primary colour-pattern on the wings of the butterflies by J. F. VAN BEMMELEN (1890), the investigations by SPULER (1892) of the wingveins and by WALTER (1885) and CHAPMAN (1893 B) of the active mandibles of *Micropteryx* are the most striking proofs, of how many important and successful investigations could still be made in the morphology of the Lepidoptera, in the last decades.

W. MÜLLER's (1886) treatise showed us the constancy in the arrangement of the so-called primary hairs of the Nymphalid-caterpillars. In a supplement this writer points out, that the same pattern occurs also in other families.

At Prof. J. F. VAN BEMMELEN's suggestion I decided to investigate how far this assertion holds good for different families. My purpose was to find an answer to the following questions:

1°. Does a conformity exist between the different colours, the pattern and the skin-relief of the caterpillars of the Rhopalocera, perhaps also of the Heterocera?

2°. Is it possible to deduce from this conformity a general plan of the caterpillar pattern, and if so, does this possess a metamerie character?

3°. Can any connection be found between the pattern of caterpillars and that of pupae, perhaps even with the colourpattern on the body of the imagines?

In thinking these questions over, I soon found that the following points are connected with the former three, viz:

4°. Is the arrangement of the hairs on all segments the same or is it different; and in the latter case, what are the relations of these differing segments in other anatomical respects?

5°. Is the arrangement on one individual in all stadia the same?

6°. Have all the individuals of one species the same pattern?

Not until I had solved these last questions, could I expect to find an answer to the first three. A priori I might expect a certain constancy of the setal pattern. The investigations by DE MEYERE (1894) of the hairs of the mammals, by MEGUSAR and WERNER of the spots on *Salamandra maculosa*, gave rise to the supposition that here also a constancy might be expected. In the beginning of August 1914, I was not yet acquainted with the extensive literature on the setae of the caterpillars. SPULER's remark (1910, p. VII) did not make me think that the primary pattern would be maintained with such pertinacity.

The 6<sup>th</sup> question I could drop very soon, as it appeared that the fluctuation or individual variation (PLATE, 1914, p. 148) is so insignificant, that it might practically be neglected. This fact apparently so simple, indicates already the great constancy of the pattern of caterpillars (see however *Papilio machaon*). During my investigation it turned out that not all the colours of cater-

pillars can stand the influence of alcohol. I therefore had to confine myself to the arrangement of the setae. For the solution of the third question I could only collect a few data which will be mentioned under the species of which I have examined the pupae. In chapter VII I intend to come back to this point. As only those naturalists, who have a very extensive collection at their disposal can fully solve this problem, I am obliged to leave the further investigation to others.

In working out the different questions I became convinced that the 4<sup>th</sup> and the 5<sup>th</sup> are the cardinal points of the investigation. Through the 4<sup>th</sup> question especially I came into contact with problems, which entirely differed from those I had originally thought of. Here too I wish to thank Prof. J. F. VAN BEMMELEN for the manner in which he encouraged me to enlarge the subject of my investigations, and for the way in which he inspired me with interest for it and also for his kindness in assisting me with his knowledge of the extensive literature.

## § 2. Material and Method.

There are a great number of books about caterpillars, with coloured and uncoloured figures, but most of them are unsuitable for my purpose. In general the figures of caterpillars are still more inaccurate than those of their imagines, of which VAN BEMMELEN said (1913, p. 107), that he found one great difficulty in his work on the colourpattern of the body of Lepidoptera, viz: that neither most of the existing figures of butterflies and moths, nor the dried specimens of the collections were suitable for a more exact analysis of this part of their colour-pattern, and that this was the same with the very few figures of the nymphs and caterpillars in the entomological illustrated publications. I cannot but agree with these words, making an exception for PACKARD'S standard-work on the Bombyces (1895—1914). As it would be too expensive to make such large photographs of each caterpillar as VAN BEMMELEN did for the nymphs of *Papilio machaon* and *podalirius*, *Vanessa io*, *Pieris brassicae* and *napi*, *Aporia crataegi*,

*Euchloe cardamines*, *Gonopteryx rhamni* and *Thais polyxena*, I have only made Indian ink drawings, with the aid of the „Zeichenapparat nach Abbe (Zeiss. Jena).” For the composition of the plates, these enlarged drawings were all reduced to the same size:  $\pm 10$  cm., by photographic reproduction. In consequence the smaller and younger specimens are represented on a much larger scale than the bigger and full-grown animals, but their actual size can always be accurately ascertained by the scale given with each figure.

These figures have the advantage that they reproduce the real aspect of the animals.

The implantation and in most cases also the length of the setae has been traced exactly from the fresh or conservated specimens. Except where a homogeneous spreading of the setae occurred and I had to work according to a scheme, I could always use this method. This method of drawing from life with a magnifying apparatus, and of reducing these enlarged figures to a certain standard length, seems to me preferable to that followed by Tsou (1914). This writer describes a method by which the length and the breadth of the setae can be determined. In chapter II I shall refer to his work.

In my method, which has also been applied in PACKARD's work on the Bombyces (1895—1914), the growth in length becomes so to speak eliminated, and therefore the variations of the pattern become more distinctly visible. At the same time these figures can be used to study the growth in thickness of the successive segments in the different instars, as the correlations of growth fully deserve to be studied further. I believe that up till now only the head has been studied in this manner. The well-known leaps in the changes of the size of the head have often assisted me to determine the moment of the moult, in cases where this was not mentioned with the preserved material. Many investigators have only turned their attention to the fullgrown caterpillars. It therefore seemed to me an interesting subject to examine the placing of the setae in all instars as accurately as possible. The difference of the results of my investigations and of those of many

others must be attributed for a great part to their not having examined the younger instars.

I should have liked to study the living animals only, but this proved to be too difficult. Therefore the animals were nearly always preserved in alcohol of 96%. As I have already said, this causes the colour to disappear for the greater part. Nearly the whole material has been cultivated in the Zoological Laboratory in the University of Groningen. Mr. E. THEYSSEN, the attendant of the Laboratory, was charged with the care of the living animals and with preserving them; and here I wish to thank him for the trouble he has taken. Before the investigation the preserved caterpillars were soaked in glycerine-gelatine. A certain quantity of this substance in a solid state was placed on the object-glass, on which the caterpillar also lay, moistened by alcohol. The glycerine-gelatine on the object-glass was somewhat heated till it became entirely liquid, when it mixed with the alcohol. Thus I obtained preparations which did not shrivel up and which on the whole kept very well. Very thick caterpillars had to be examined in a dry state or lying in a watch-glass with alcohol, sometimes after the hairs had been cut very short.

Besides this material I could dispose of the magnificent collection of Dr. F. W. O. KALLENBACH at Apeldoorn. This very rich collection has been presented by the collector to the Zoological Laboratory in the University of Groningen. Besides the numerous imagines it contains the mounted and dried caterpillars of most of the species and of many even more or less complete series of the stages of development. The specimens which I have used are indicated by *Coll. Kall.* Many entomological plates I have looked through, and though the objections already mentioned could not be discarded, the figures sometimes gave valuable indications as to the direction in which the further investigation had to be made. The works indicated with an asterisk give the most correct figures and descriptions. As a proof of the unreliability of the figures in scientific entomological works, I draw attention to the figure Taf. III, fig. 38 in WEISMANN's before mentioned study

of *Deilephila euphorbiae*, which bears a stigma on the mesothorax as well as on the metathorax.

A list of the illustrated works I consulted follows, the exact titles are to be found in the bibliography; the date given refers to the beginning of the publication.

DE RÉAUMUR 1737.	*BUCKLER 1886.
SEPP 1762.	SCUDDER 1888.
HÜBNER 1786.	HOFMANN 1893 see SPULER.
RATZEBURG 1840.	*PACKARD 1895.
DUPONCHEL 1849.	BEUTENMULLER 1900.
HORSFIELD and MOORE 1857.	FORRESTER 1907.
*MILLIÈRE 1858.	TONGE 1907.
WILDE 1861.	*SPULER 1910.

In chapter VI I have given a systematic synopsis of the caterpillars which I have examined. Of those families, of which I had no specimens at my disposal, I have given an account taken from the literature on the subject.

## CHAPTER II.

### LITERATURE.

The studies by WEISMANN which I have mentioned before, were made to prove the correctness of the ideas introduced by DARWIN on the transformation of the organisms. He had two reasons for his choice of the pattern of caterpillars as a test-object for his theoretical conceptions:

1. because with them sexual selection is out of the question.
2. because only the colouring of caterpillars was considered to be of value for the life of their bearers and not the pattern, which has nothing to do with the colour.

For special reasons WEISMANN confined himself to the *Sphinxidae*. His terminology is as follows:

1. Linea dorsalis, placed in the middle of the dorsum.
2. Linea stigmalis or linea suprastigmalis and infrastigmalis.
3. Linea subdorsalis, just between 1 and 2.

It is well known how WEISMANN brought back the eye spots and the ringed spots to the linea subdorsalis. He distinguishes four ontogenetic and phylogenetic stages in the course of development of the colourpattern during larval life.

Stage I. Green, without any pattern.

Stage II. Subdorsal line, sometimes also a dorsal and a stigmal line.

The biological value of this stripe was that it divided the strikingly large body of the caterpillar into parts and in that way made it less conspicuous.

Species showing this longitudinal striation lived on grasses and conifers.

Stage III. Cross stripes l. c. p. 127.

New characters arise only during the ultimate stages of the larval life and when new ones are developed, they disappear from the last stage and arise in the former one. The character of the cross stripes becomes completed by accompanying coloured borders (shadow).

Stage IV. The eye spots (with a dark pupil = central spot, a bright shining spot and a dark ring) and the ringed spot (without central spot) arise from or in connection with the subdorsal line, on the fourth and fifth segment of *Chaerocampa* (l. c. p. 97) and on the eleventh caudal-horn segment of *Deilephila*. The spotted pattern is a warning colour. WEISMANN was able to point out a biological meaning for these three principal elements of the sphingidal pattern and thus he could explain their origin by natural selection. For the explanation of the repetition of a locally originating pattern on the other segments, however, he had to refer to the rule of correlation (l. c. p. 136).

WEISMANN declares positively that the first stage has no pattern e. g. *Deilephila euphorbiae* (l. c. p. 25). „When, however, the youngest larvae of this species are scrutinized with a high power, it is seen that from the beginning they are dark-green, while the horn is black, so also are the head, the feet and a semi-circular chitinous shield on the dorsum of the prothorax and one paired and two unpaired chitinous shields on the last segment.

As yet no trace is to be found of the pattern, which appears later on. The stigmata are visible as white spots. On each segment there is a number of warts (in most cases ten) each of which bears a simple bristle. When the small caterpillars have obtained a length of 7 mm. they are olive-green and no longer form such a great contrast with the green *Euphorbia* leaves as before; still they do not possess any definite pattern. After five days the first moulting takes place and with it a very complicated pattern suddenly appears (fig. 38—39)."

WEISMANN also mentions a full-grown *Smerinthus* (?) species in the museum in Berlin of which he says, „that it is sparsely covered with bristles but does not show a trace of any pattern, and agrees all the more with the youngest stage of most of the now living *Spingidae* as it also has short bristles thinly spread over the surface of the animal. This „living fossil” had a length of 6 cM.”

For the rest the pattern of the hairs resembles that which I found amongst others in *Sphinx ligustri* and *Smerinthus tiliae*.

WEISMANN's classical treatise has rightly met with much appreciation but, unfortunately, has found too little imitation.

For a more exact insight into the system of the Lepidoptera a complete knowledge of caterpillars will without doubt prove to be of great value.

The accuracy of WEISMANN's investigations and the great keenness with which he has deduced very comprehensive theories from apparently unimportant facts, guarantee to his work a prominent place in zoological literature.

In his next study WEISMANN (1876 II<sub>2</sub>) discusses the so-called „parallel rows”. He starts from the following argument (l. c. p. 141):

„If the development of the organic world depends upon a phyletic vital power, there must have taken place and still be taking place what I call „phyletic parallelism”, i. e. the development of the two stages of metamorphic species must have taken place in exactly parallel direction; each transformation of the butterfly would have been accompanied or followed by a transformation of the caterpillar, and the systematic groups of the butterflies would

be found again in just the same way in a system of the larvae, or in other words: the relation of forms of the caterpillars must harmonise precisely with that of the butterflies."

"If the development is only the reaction of the specific organism to the influence of the outer circumstances, dissimilarities in the phyletic development of the different stages of life might be expected" ... A congruency might be the consequence of correlation.

WEISMANN goes on to say (l. c. p. 157) "that the primitive cause of variations when coming from outer circumstances must occur far oftener with larvae than with butterflies."

DARWIN points out the heridity in corresponding ages or as HAECKEL calls it: homoehronic heridity.

WEISMANN thinks he has here found an explanation for the great differences between larva and imago (p. 168) „as the acquirements of the separate stages in the following generations are always transferred to those stages themselves but the other stages remain untouched”.

After having discussed the different families, to which I shall return later on in discussing the groups, WEISMANN comes to the following conclusion: „there is a great congruency between the system of larvae and that of imagines, especially where the genera are concerned, but the incongruencies appear mostly with varieties and families”. To the questions, what may be the cause of the difference in form of butterflies and moths being so much greater than that of their caterpillars, and why the imagines of the Rhopalocera have so many characteristics in common which their caterpillars do not possess, WEISMANN gives the following answer (l. c. p. 195): „that this might be explained by the great differences in the manner and duration of life of the imagines.”

WEISMANN's study was followed by a great many others, some of which I intend to discuss with the families. Here I will only give a short index of those which are of general importance.

WILHELM MÜLLER is the first (1886) who pays special attention

to the arrangement of the „hairs” on caterpillars. It is true that DE RÉAUMUR had pointed out in 1736 the peculiar warts of different caterpillars and the plumed hairs they bear, also that MILLIÈRE added a drawing of the back part of the body with the hairs on the last three segments (1858 I, Pl. I, fig. 4) to his description of *Coccyx junipera* Mil., but no systematic investigation of the arrangement of the hairs had, as far as I know, taken place before W. MÜLLER.

Before going further I wish to observe that the „hairs” of the insects are mostly developed as offshoots of a hypodermis-cell. They are absolutely different in construction from the hairs of mammals and therefore the word *setae* has been introduced for them by LANKESTER. Consequently I shall only use the word „hairs” in this study, in cases where the writers quoted do not mention the word *setae* for some reason or other. FRACKER (1915, p. 38) thinks that the *setae* are sensory in function. As with all kinds of other organs the form of the *setae* of the caterpillars often gets more intricate after each moult, so that it is of great importance to examine all the succeeding stages, and thus to get a good insight into the covering of the skin of the full-grown caterpillars. To avoid confusion between the two meanings of the word stage (the caterpillar or larval stage, the pupal stage, and the period between two moults of caterpillars), FISCHER has introduced the term *instar* for the last mentioned meaning. The larval stage therefore consists of several *instars*.

MÜLLER began to pay attention to the first instar of the Nymphalid-larvae. In them he discovered a constant arrangement of the so-called „primary bristles” which he gave the numbers 1—6 (see Nomenclature). Bristle 6 only occurs on the segments 2—5 and 10—12.

The segments 1, 2 and 3 (the thoracic rings) are different and so is segment 12. A comparison of the bristles proves that there is a special segment 12*a*, but this only exists during the first instar. It is very easy to homologize the bristles on the segments 4—12 (the abdominal ones) but the mesothorax and metathorax are widely different, a shifting may perhaps have taken

place in their arrangement in connection with the development of the wings and the disappearance of the stigmata. To this I shall refer again in chapter V.

Just before the first moult white spots glimmer through the skin, some of which will grow into secondary bristles (scoli) and others are destined to become the white warts which are the cause of the pattern.

The starting point of these secondary bristles does not coincide with that of the primary ones (l. c. p. 110 and fig. 14, Pl. 3), very often they are median and consequently unpaired, which is never the case with the primary ones (See Pl. 1, fig. 1).

The pattern of the caterpillar often passes on to the pupa, the cuticular pigments disappear and the subcuticular ones remain (l. c. p. 231).

In contradistinction to WEISMANN, MÜLLER (l. c. p. 232) says that the new characteristics which have appeared during the larval stage are shifted on to the pupal stage and the other way about.

With each moult the scoli of the *Nymphalinae* get more and more intricate. He calls them after the line on which their base is fixed. In an appendix MÜLLER mentions the observations on the origin of the scoli known up to that time (l. c. p. 250), and also shows that the pattern of the primary hairs is found again in other families. He then says:

Spines arise:

1. As independent elevations, without any relation to setiferous warts: horns of the *Nymphalidae*, pseudo-spines of *Caligo* and *Danais*, gills of *Cataclysta* and *Paraponyx*.

2. By transformation of warts bearing bristles; viz.:

a. Of the warts of primary bristles, probably the most common method (forked tail of the *Satyridae*, pseudo-spines of the *Papilionidae*, spines of the *Saturniadae*, tail-horn of the *Sphingidae*).

b. Of the warts of the secondary bristles (spines of the *Nymphalinae*).

The biological meaning of the spines cannot be for defence against caterpillareaters (l. c. p. 93), for caterpillars with large

and numerous spines are persecuted just as much as those without them.

In his derivation of the spines from the secondary bristles and not from the primary ones, MÜLLER is in contradiction with GRUBER (1884). In a discussion of the American *Papilionidae* and *Nymphalidae* GRUBER says (l. c. p. 476). „The *Papilionidae* often possess in the first instar warts with spoon-shaped setae and sometimes with forked ones which become smaller during the moults and which have sometimes totally disappeared after the first moult.

„The *Nymphalidae* have small bristles in the first instar, each apart on an elevation and later on we see large warts with numerous bristles, completely agreeing in number and place with the elevations of the first instar. (See *Papilionidae* and *Nymphalidae*, Chapter VI)“.

SCUDDER (1888) too gives a description of the caterpillars.

He names the setae, spines etc. after the lines which connect them with each other and he distinguishes twelve paired and two unpaired lines viz. the *dorsal* or *mediodorsal*, *subdorsal*, *laterodorsal*, *supralateral*, *lateral*, *infralateral*, *laterostigmatal*, *suprastigmatal*, *stigmatal*, *infrastigmatal*, *ventrostigmatal*, *lateroventral*, *subventral*, *ventral* or *medioventral*.

The italicized lines divide each side of the body in three parts which are about equally large.

SCUDDER (p. 12) observes: „All of our butterfly caterpillars are clothed with hairs . . . , their arrangement affords admirable generic characteristics which have not hitherto been sufficiently appropriated. It should be stated that juvenile caterpillars in their first stage may be safely said to differ generically from themselves at a mature epoch. The hairs, spines etc. are placed in transversal and longitudinal rows, the former are subordinate to the latter“.

On p. 235 SCUDDER says his opinion on the ancestors is that the surface of the body was profusely covered with little papillae from each of which sprang a minute simple hair. In harmony with this he says that the wings too of the first butterflies were uniformly dark brown. In the course of this paper I hope to prove that a homogeneous spreading of the setae is not a primary

feature, whilst for the colour of the wings of Lepidoptera I refer to J. F. VAN BEMMELEN (1889—1916), J. BOTKE (1916), J. H. DE MEYERE (1916).

The next study which is of great importance for the knowledge of the setae is that of PACKARD (1890). Without paying much attention to the arrangement of the setae, PACKARD especially devoted himself to their different shapes. What struck him especially with the Bombyces, was the intricate shape of the setae of the full-grown caterpillars. He examined their ontogenesis and thereby was led to the establishment of a series of types (l. c. p. 512 sqq.) of tubercula and setae which are often used even now in descriptions. PACKARD's list, which has also been included in the great work (1895) on the Bombyces, may be cited here:

#### „A. Tubercles.

a. *Simple and minute*, due to a slight thickening of the hypodermis and a decided thickening of the overlying cuticle; the hypodermis contains a large unicellular gland either for the secretion of the seta or for the production of poison.

1. Minute piliferous warts (Most *Tineid*, *Tortricid* and *Noctuid* larvae).

2. Enlarged smooth tubercles, bearing a single seta.

(Many *Geometrid* and *Bombycine* larvae).

3. Enlarged, spherical tubercles, bearing a number of setae, either radiated or subverticillate (*Arctians*, *Lithosians*, *Zygaenidae*, including some *Glaucopinae*).

4. High, movable, smooth tubercles, having a terrifying function (*Schizura*, *Xylinodes*, *Notodonta*, *Nerice*).

5. Low and broad, rudimentary, replacing the „caudal horn” (*Choerocampa*, the European *Pheosia dictoea* and *dictoeoides*).

b. *More or less spinulose or spiny* (disappearing in some *Sphingids* after stage I).

1. Long and slender, usually situated on top of the eighth abdominal segment, with microscopic spinules in stage I. (Most *Sphingidae* and *Sesia*).

2. Smooth, subspherical warts (*Zygaenidae* e. g. *Chalcosia*, East Indies) or elongated but still smooth (*Attacus atlas* and a species from South-western territories U. S. A.).

3. Subspherical or clavate, spiny tubercles of many *Attaci*, the spinules usually short.

4. Spinulated spines or elongated tubercles of *Ceratocampidae* and *Hemilucidae* (*H. io* and *H. maia* etc.).

5. Spikelike hairs or spines (*Samia cynthia*, *Anisota*, East-Indian *Hypsa*, *Anagnia*).

6. Antler-like spines. Early stages of *Heterocampa biundata*, *guttivitta* and *obliqua*.

#### B. Setae („hairs”, bristles etc.).

1. Simple, fine, short or long, microscopic or macroscopic setae, tapering hairs, scattered or dense, often forming pencils (Many *Bombyces*, *Zygaenidae*, *Noctuobombyces*, *Apatelae*).

2. Glandular hairs, truncate, spindle-shaped or forked at the end and secreting a more or less viscid fluid (Many in stage I and II of *Notodontians*, many *butterfly-larvae* and in the last stages of *Pterophoridae*).

3. Long, spindle-shaped hairs of *Apatelodes*, *Apatela americana*, and the European *Tinolius eburneigutta* Walk.

4. Flattened, triangular hairs in the tufts or on the sides of the body of *Gastropacha americana*, or flattened, spindle-shaped scales in the European *G. quercifolia*.

5. Spinulated or barbed hairs. Most *Glaucopides*, etc. *Arctians*, *Lithosians* and *Liparidae* and many other *Bombyces*.

#### C. Pseudo-tubercles.

1. The filamental anal legs (stemapoda) of *Cerura* and *Heterocampa morthesia*.

2. The long suranal spine of *Platyptericae*.”

PACKARD's view on the origin of these different forms is the following (1890 l. c. p. 560):

1. The more prominent tubercles and spines or bristles arising

from them, are hypertrophied piliferous warts, the warts with the seta or hair which they bear being common to all caterpillars.

2. The hypertrophy was probably primarily due to a change of station from herbs to trees, involving better air, a more equable temperature, perhaps a different and better food.

3. The enlarged and specialized tubercles developed more rapidly on certain segments than on others, especially the more prominent segments, because the nutritive fluids would tend to more freely supply parts most exposed to external stimuli.

4. The stimuli were in great part due to the visits of insects and birds, resulting in a mimicry of the spines and projections on the trees, the colors (lines and spots) were due to light or shade, with the general result of protective mimicry or adaptation of tree-life.

5, 6, 7, 8 and 9. Through heredity these first steps in the evolution, in the beginning due to primary factors of evolution (Neo-lamarckism) became constant, due to segregation and natural selection, because intercrossing with low feeders would cease.

As the probable time of the origin of the large setae and warts PACKARD mentions: „the critical time attending or following the close of the Palaeozoic or the early part of the Mesozoic age, the time when deciduous trees and flowers probably began to appear” (l. c. p. 506).

In 1893 PACKARD refers again to this subject, in which he thinks he has found a basis for a natural classification of the Bombyces (see chapter VI).

DYAR independently of W. MÜLLER, examined the primitive pattern in 1894 and has even made an analytical list for determinations according to the setae.

As for the nomenclature I refer to Chapter V. His table follows here.

Synopsis of the Families of Lepidopterous Larvae.

- A. More than one tubercle on the third annulet and more than three on the base of the leg. — *Jugatae*, *Hepialidae*.  
 A.A. Not more than one tubercle on third annulet and only six above the base of the leg. — *Frenatae*.

B. Three tubercles on middle annulet, none on the third.

Tubercles IV and V approximate, two thoracic shields.

*Psychidae*.

BB. No more than two tubercles on middle annulet and usually one on the third annulet, one thoracic shield (prothoracic).

C. Tubercles IV and V approximated or consolidated.

*Generalized Frenatae*.

D. Tubercles simple, single haired. *Cossidae*, *Pyralidina*, *Tortricina*, *Tineina* (in part), *Lacosomidae*, *Sesiidae*.

DD. Tubercles absent, as well as legs. *Tineina* in part.

DDD. Tubercles modified, many haired.

E. All present but tubercle I. *Pterophoridae*.

EE. Subventral tubercles also reduced, only three left. *Pyromorphidae*, *Megalopygidae*.

EEE. Substigmatal tubercles absent, only two left.

*Eucleidae*.

CC. Tubercles IV and V remote (sometimes IV disappeared and then essentially the same arrangement as in EEE.)

*Specialized Frenatae*.

F. Tubercles all present or with a slight tendency to unequal reduction, setiferous or equally reduced.

G. Simple with a single seta: *Noctuidae* (in part).

*Agaristidae*, *Notodontidae*, *Geometridae*, *Drepantidae*, *Lithosidae* (in part).

GG. Tubercles with many hairs.

H. Without any development of hairs from the skin. *Noctuidae* (in part), *Pericopidae*, *Arctiidae*, *Euchoniidae*, *Zygaenidae*, *Lymantridae*.

HH. Tubercles greatly reduced, abundant hair from the skin. *Lasiocampidae*.

FF. Tubercles with marked unequal reduction or greatly modified or absent.

I. Tubercles still wartlike, hairy. (The young larvae of many *Papilionidae* will also come in here).

II. Tubercles greatly modified or absent.

J. Tubercle I normal (when present).

K. Tubercles produced into naked fleshy horns or represented by coloured spots. *Papilionidae*, *Nymphalidae* (in part).

KK. No trace of tubercles. *Nymphalidae* (in part), *Pieridae*, *Hesperidae*.

JJ. Tubercle I consolidated with its fellow on the dorsum.

L. No unpaired dorsal tubercle anterior to abdominal segment 8.

M. Tubercles largely present. *Saturnia*.

MM. Only the dorsal tubercle on segment 8. *Sphingidae*.

LL. A line of unpaired dorsal tubercles throughout the length of the abdomen, anterior to segment 8, or largely so. *Nymphalidae* (in part).

What strikes us in the first place in this list is that several families belong partly to one group, partly to quite a different one. This might indeed be expected in an artificial system like this. In the second place we see that the determinations of many families with the aid of this table will prove to be difficult e.g. the *Pieridae*, which are densely covered with setae, and which, though their primitive pattern remains visible for a long time, are said by DYAR to present: „no trace of tubercles”.

The artificiality of such a classification is evident.

I think that DYAR in this case was under the influence of COMSTOCK'S suggestive paper (1893), and that he exerted himself to find a characteristic in the caterpillars, which allowed him to apply COMSTOCK'S division of Lepidoptera into *Jugatae* and *Frenatae* to the larvae also.

My third and main objection is that except in group I no attention has been paid to the ontogenesis. Where the setal pattern undergoes rather important modifications during the larval stage and some members of the family remain on a lower scale of

development (as a classical example I cite the *Sphingid* with a complete setal pattern, mentioned by WEISMANN), there it is absolutely certain that a classification like this must prove to be inefficient as soon as a great number of different forms of one family are compared with each other. FRACKER who in 1915 once more tried to compose an analytical list for the determination of caterpillars, has been obliged to use other characteristics, such as the rows of crochets on the abdominal legs. At the same time FRACKER very logically begins with the most generalized families and gradually passes to the most specialized ones (l. c. p. 49—59). FRACKER'S main classification is no longer based on the setae but on other characteristics. He introduces a completely new nomenclature, against which I intend to raise my objections in a following chapter. It is a great pity that, where he apparently had extensive material at his disposal, he paid so little attention to the ontogenetic changes of the setal pattern. During the discussion of the different families I shall have to point out some mistakes in FRACKER'S work (see e. g. *Pieridae*, *Bombyx mori*, *Porthesia chrysorrhoea* etc.).

TSOU who worked at about the same time as FRACKER, published a method in 1914 for determining the length and the breadth of a seta on the segment. He examined almost exclusively a full-grown *Cossus cossus*, *Hepialus humuli* and *Jaspedia celsia*. He chooses the prothorax as point of issue for his deductions, on the not quite scientific ground that it is the first segment of the body. (l. c. p. 228). He also groups the setae in a peculiar way of which he himself admits that it is more or less artificial. I cannot but agree with him in this qualification. As I do not agree with his method of comparing fullgrown caterpillars of different families with each other without attending to the first instars at all, nor with his taking the prothorax as the starting-point, nor with his uniting the setae to arbitrary groups, I think that here it is sufficient simply to mention his work.

O. HOFMANN in 1898 devoted a study to the caterpillars of the *Pterophoridae*. DYAR had brought forward the great systematic

value of the setal pattern, but O. HOFFMANN came to the conclusion that in a perfectly natural family like the above, the primitive pattern showed great divergences. In discussing the family I shall return to this. A general importance is granted to this study by A. SPULER (1910), who writes on p. VII of the fourth volume of his well-known book on butterflies and caterpillars, that the setal pattern is evidently not of such great value as DYAR believes.

J. TH. OUDEMANS on p. 384 of his excellent work on the Dutch Insects (1897—1900) remarks, in general terms, on the hairs as they usually occur on most caterpillars.

He does not touch on their systematic value.

AMBROSE QUAIL's notes on *Cossidae* 1904<sup>b</sup>, [he uses these animals i. a. to determine the number of the abdominal segments (10),] are followed by some general remarks. He divides the caterpillars into three groups. I. c. p. 269.

I. single seta-tubercles in all stages. *Hepialidae*, *Cossidae*, *Noctuae*, *Geometrae*.

II. single seta-tubercles only in first stage: *Pieridae*, *Sphingidae*, *Nymphalidae*, *Arctiidae*.

III. More rarely in first larval stage some tubercles with more than one seta. *Liparidae* etc.

After his attention had been drawn to it by Mr. A. BACOT (footnote p. 95) he says in his second treatise I. c. p. 270:

„I submit the homologue of II B of the thorax is a minute anterior supraspiracular tubercle of the abdomen called by me III B, that DYAR's III of the thorax = a sub-spiracular tubercle of the abdomen and so on." I shall refer to this in chapter IV.

FORBES in 1910 and 1911 also gave attention to the problems I have just discussed. I regret not having been able to obtain these papers. In the chapter on nomenclature I have discussed what information I got about them from the quotations of other writers.

It is peculiar that though DYAR as early as 1894 homologized setae and tubercula with the pigmental spots, it was not before

1912 that J. F. VAN BEMMELEN succeeded in proving this suggestion. This writer found that the pattern of the caterpillars of *Pieris brassicae* might be retraced in the design of the pupae. He then could recognize the same pattern on pupae of several other *Pieridae* and also of *Papilionidae* and *Nymphalidae* and even succeeded in discovering it on the bodies of the imagines.

In a following chapter (VII) containing the discussion of the pupal pattern, I shall return to this important question.

It is perhaps due to the influence of WEISMANN and EIMER, who considered the linear-pattern as the original one, that insufficient attention is paid to theories which regard the spotted pattern as the most primitive.

It is certain that SCHRÖDER (1894) in his study of the *Geometridae* has been too much influenced by this preconceived idea. This investigator has paid still less attention than WEISMANN to the setae bearing tubercles and consequently has quite overlooked the pigment accumulation at the base of the setae. For the discussion of the origin of the linear pattern and the primitive character of the spotted pattern I refer to chapter IX.

J. C. H. DE MEYERE in his recent paper (1916) arrives at conclusions which are in general the same as mine. In chapter VI and VII I shall return to his paper.

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## CHAPTER III.

### ON THE STRUCTURE OF THE THORACIC SEGMENTS.

In several respects the construction of the thorax differs from that of the abdomen, a difference which very early attracted the attention of entomologists. Before discussing my nomenclature, I prefer to investigate, which segments are the most primitive ones, in other respects than the covering with setae. There are reasons for supposing that segments of primitive construction in other respects, will also display this original character in their setal pattern. I cannot avoid mentioning many facts which

are generally known. As however the investigators, who have written on the setal pattern, have not paid any attention to these familiar facts, I think it may be useful to recall them to memory and point out their connection with the arrangement of the setae.

The first who, I think, remarked the wing-rudiment in caterpillars, was JAN SWAMMERDAM, who described it in *Biblia Naturae* II, p. 615 and in 1668 showed it to the Duke of Toscane, to Thevenot and to Magalloti. He described it under the title of: „Animal in animali or the butterfly hidden within the caterpillar.”

The same thing is found in *Historia generalis* p. 202 as: „Insectum in Insecto seu Papilio in Eruca”. In both cases *Pieris brassicae* was the object of the investigation. The next investigator who mentioned the wing-rudiment was P. LIJONET who in 1760 wrote his famous „Traité anatomique” and on p. 592 says: „The isolated figure towards the bottom of the middle of Pl. XI is a mass of white satin-like stuff, placed in fat without sticking to it and which is attached in B to the inner membrane of the skin.

There are four such lumps within the caterpillar (*Cossus*), they are found on either side of the 2<sup>nd</sup> and 3<sup>rd</sup> rings. They might be the origin of the wings of the moth”. And on p. 449: „It is attached to the skin in the deep fold which it makes”.

With his well-known accuracy LIJONET draws many more muscles in the thorax than in the abdomen and many of them are not connected with the thoracic feet. — I think therefore, that other differences besides these legs have been established between the thorax and the abdomen, so that HENNEGUY's contention (1904, p. 442), that in legless larvae all the segments have exactly the same constitution, can only refer to external features.

The presence of the wing-rudiment combined with the absence of the stigmata has induced many students to consider the wings to be modified tracheae.

But a good many investigators who later on have examined the development of the wing, have come to the conclusion that the first change does not start from a trachea but from the skin.

As the principal studies on this subject I may mention those of LANDOIS 1871, GANIN 1876, PANCRITIUS 1884, DEWITZ 1887, VAN BEMMELEN 1889, BUGNION 1892, GONIN 1894, MAYER 1896, MERCER 1900, BAUER 1904, v. VOSS 1912.

GONIN's work especially is often cited. He examined in the first place *Pieris brassicae* and says (1894) of the origin of the so-called *disque imaginal* that it is better to use the term *repli imaginal*.

I wish to point out the concurrence between him and LIJONET. „The *repli imaginal* originates from evagination of the hypodermis, preliminarily invaginated. The part which the tracheae and the nerves play in this formation is a secondary one. The tracheae are neither the cause of the duplication nor of the extension of the walls of the wing. The rudiments of the wings are developed from the first larval age but do not participate in the larval moults, their surface does not produce a cuticle till towards the end of the last stage”.

MERCER who I think, has been one of the latest investigators of these organs, has found in *Pieris* also that the rudiments of the wing grow.

In a few words his results may be summarized as: instar *I*, over against a trachea a thickening of the hypodermis is found, in the middle of which lies a cavity, and round the trachea some detached cells (= lymphocytes?). Instar *II*, a chitinous plug penetrates into the cavity; Instar *III*, the wingbud arrives in the body cavity, but remains connected with the hypodermis by the „peripodal membrane” (v. REES). The trachea becomes larger and grows into the two layers of the hypodermis. Instar *IV*, the tracheoli enclosed in the wing-bud reach the edge. Instar *V*, the tracheoli grow further, the „wing-rudiment” reaches the leg and becomes folded. Pupa, the larval tracheoli disappear and are replaced by a quite different pupal system.

BAUER (1904) adds to this that the form of the wing-folds is only governed by mechanical forces. If the thick larval cuticle is an obstacle, the fold becomes invaginated, but directly evagi-

nates and becomes an elevation as soon as this obstacle is removed. This explains the so-called „vorzeitige Entwicklung” (premature development).

Consequently in the beginning the wing-rudiment is not connected with the tracheae and in instar 1 the rudiment of the wing is only a minute thickening of the hypodermis. This knowledge will be of much use to us in discussing the so-called rudimentary stigmata on the mesothorax and metathorax.

The way in which the thorax is provided with stigmata is a second point which I wish to discuss. There are many different opinions on this subject.

In his description, which for the rest is exceedingly accurate, of *Cossus* (Traité de la chenille, 1760) LIXONET does not mention the rudimentary thoracic stigmata. The remaining stigmata he points out very accurately and also their connection with the „bronchi” as he calls the tracheae. It is peculiar that he does not fully believe in their respiratory function in consequence of the experiments mentioned by him on p. 78.

A. C. OUDEMANS observed (1886, p. 19) that the Myriapodae and Hexapodae always bear the stigmata within the limits of the segment itself, but he admits that in adults they can be shifted either to the front part of the segment or to its back part and in so doing may even get into the intersegmental membrane.

In direct opposition to this stands HENNEGUY's contention (1904) that the stigmata generally occur intersegmentally, but that later on this position may be altered. He ascribes this to the complimentary segments which KOLBE discovered. This writer says that in the beginning no stigmata occur on the head and the prothorax (l. c. p. 20). With this the models of *Hydrophilus piceus* L. (manufactured in the studio of ZIEGLER according to K. HEIDER's treatise, 1889) are in perfect harmony. Here it is clearly visible that the first stigma appears on the mesothorax (Stage 9, model 9).

For a student, who has not yet undertaken any special investigations in this direction, it is exceedingly difficult to find out the truth. A priori one would be inclined to think that both

opinions can be true for different objects. In the literature I found some papers which specially treat this question. It is a pity that the last-mentioned writer KÜMMETH, apparently was not acquainted with BOAS' paper.

BOAS devotes p. 390 of his article (1899) to the question of the thoracic stigmata. Relying on his examinations of *Cossus ligniperda* and *Ergates faber* (a Cervicornid) he says that there are two thoracal stigmata. The first is shifted to the prothorax, the second forms a closed, rudimentary stigma in the intersegmental membrane between the mesothorax and the metathorax. This rudimentary stigma is situated lower than the ordinary ones. The so-called rudimentary stigmata, lying in the stigmal line, are in reality the origins of wings. In the imago the closed larval stigma becomes open.

TOWER (1906) found in *Leptinotarsa* „that the wing in development starts from a minute invagination of cells in the region of the wing spots, which is an area, as shown by VERTON, myself and others, homologous to the spiracular centre of other segments (l. c. p. 163).”

G. C. CRAMPTON (1914) does not enter into this question. He is unwilling to accept the assumption of subsegments in the thorax, since he is convinced that all theories about the compound-segment are unfounded (p. 56).

JANET (1909) gives a very interesting list of the origin of the different segments and subsegments.

From this I only quote: (see also Chapter IV, p. 27).

Ordre ontogénique.	Ordre anatomique.		
13	10	prothorax	spir. prothorac. des Diptera.
15	11	mésothorax	spir. mesothoracique.
14	12	métathorax	spir. metathoracique.

We therefore see that BOAS and JANET agree with HENNEGUY in the supposition that the prothorax has no stigma of its own and that a shifting of the stigma in an oral direction has taken place when a prothoracal stigma occurs.

KEMMETH again went into this question thoroughly in 1914 and has added very accurate figures to his text (Pl. V, fig. 1—25). He has examined various orders of insects, but unfortunately, mostly as imagines. His principal results are:

The thoracic shield is formed by three thoracic segments and one abdominal segment, which, however, retains an abdominal structure. These four rings bear three pairs of stigmata, one abdominal pair as usual situated in the praesegmental zone (sometimes more dorsal: Pulicidae, sometimes more ventral: Rhynchotae) and two thoracic pairs, situated postsegmentally or intersegmentally. The first pair always breaks through the connective membrane between the prothorax and mesothorax, sometimes more prothoracally (Coleoptera, Rhynchota, Hymenoptera), sometimes more or less in the intersegmental connective membrane (Plecoptera, Lepidoptera). In Odonata, Neuroptera and Panorpata it is forced by the strong reduction of the prothorax against the praesegmental edge of the mesothorax. It is able to move considerably in the dorso-ventral direction.

The second pair of thoracic stigmata is found between the mesothorax and metathorax, mostly on a line with the first pair. In Hymenoptera and Lepidoptera it is situated directly under the root of the back-wing. This is confirmed by the larvae.

ZANDER found in 1910 that the first pair belongs to the postsegmental zone of the prothorax, the second pair to the intersegmental membrane of the mesothorax and metathorax. An exception is formed by *Dytiscus* and *Ergates*, where the first pair is situated in the praesegmental part of the 2<sup>nd</sup> segment.

There is not the least indication that formerly there were three thoracic pairs of stigmata, and that in one group one of these became obliterated, in another group another. The only thing which is certain, is that the functioning stigmata of different insects belong to different segments. The second stigma mostly lies a little ventrad.

Without making any claim to finality in this important question, I think it may be accepted as quite certain:

1<sup>st</sup> that *Ergates*, as examined by BOAS, cannot be considered as showing the general rule.

2<sup>nd</sup> that the prothoracic stigma of recent insects originally belongs to the intersegmental membrane or to the praesegmental zone of the mesothorax and that it can be shifted unto the prothorax.

3<sup>rd</sup> that the second thoracic stigma was originally situated in the intersegmental membrane between the mesothorax and metathorax, and that commonly it lies more ventrally than the other stigmata.

4<sup>th</sup> that the abdominal segments (1—8) possess a praesegmental stigma.

JANET (1909) mentions a 9<sup>th</sup> abdominal stigma for *Lepisma*, BRAUER (1851) for *Panorpa* a stigma on all the 13 segments, except on the mesothorax and metathorax.

Accepting the probability, that the homoiomery, which shows itself so strongly in Insects, originally also ruled the tracheal system, the conclusion logically follows, that in the beginning the stigmata on the thorax were also situated praesegmentally. But then we must also assume that the second pair of thoracic stigmata in reality belongs to the metathorax and the prothoracic stigma to the mesothorax. From this follows a shifting of the stigmata in the direction of the head sometimes over a considerable distance. Through this shifting the metathoracic stigma is pressed a little towards the ventral side, whilst the first thoracic stigma may at the same time turn to the dorsal side.

If this hypothesis is correct, then the whole thorax has been modified and therefore cannot have preserved a primitive structure. This assertion is supported by the different arrangement of the muscles, already described by LIJONET. VON VOSS also has pointed out the secondary structure of the thorax in his papers 1911, 1912, 1913. If therefore the primitive structure of a segment is the object of our research, we must study the abdominal instead of the thoracic segments. Herein lies a strong argument against FRACKER and TSOÜ, who take the prothorax as a starting point.

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## CHAPTER IV.

## ON THE NUMBER OF THE SEGMENTS AND ON THE ABDOMINAL LEGS.

According to KOWALEWSKY's observations on the development of *Smerinthus populi* (1871) the abdomen of insects originates from 10 somites, all of which possess a tendency to form abdominal legs. (p. 53, Pl. XII fig. 8 and 10). He was followed by TICHOMIROFF (1879) who counted 11 abdominal somites in *Bombyx mori*, likewise provided with pedes spurii, except the first. These abdominal legs also occur in other orders of insects. RATHKE showed them in 1846 for *Melolontha*, HEIDER (1889) for *Hydrophilus*. The first abdominal legs are remarkably large (ZIEGLER's Model). WHEELER observed in 1893 also 11 abdominal somites in *Xiphidium ensiferum*.

JANET in 1909 comes to a total of 27 metameres of which 9 pass into the head and 3 into the thorax, the other 15 form the abdomen. The three posterior ones which appear immediately after the first three head-metameres constitute the proctenteron. The metameres appear in triads, the first and last member of each triad always showing themselves before the middle one. The last triad is formed after the first, the others are regularly developed from the oral to the caudal side. JANET also distinguishes 12 abdominal ganglions and 3 proctentral ones in accordance with the 15 metameres.

When W. MÜLLER occupied himself in 1886 with the setal pattern, he clearly saw that the 12<sup>th</sup> segment (= the 9<sup>th</sup> abdominal) consisted of two parts which were separated by a furrow (l. c. p. 106—107). The first part develops into a nearly complete normal segment, the second part, though in fact also a special segment, is called in his description 12<sup>a</sup>. As he adds „according to tradition and owing to the circumstance that the value of 12<sup>a</sup> as an independent ring can only be proved during the first stage”.

As we are obliged to agree with HENNEGUY's contention

(1904, l. c. p. 423): „The moment of the hatching does not correspond to an exact point of the embryonic evolution. This moment is of a purely physical nature and depends on the smaller or larger quantity of nutritive reserves contained within the egg”, we may expect that in other families segment 12<sup>a</sup> will remain independent till after the first instar. The more so as in 1896 CHAPMAN was able to show so great a difference between the eggs of Lepidoptera.

Therefore we need not be surprised if some writers are convinced that there are more than ten abdominal segments, and others that there are only ten or less.

For my part I think that it entirely depends on the specimens examined.

POULTON (1890) says that „behind the 7<sup>th</sup> abdominal segment most writers only detect a somewhat confused mass of segments, but a careful comparison with the pupa proves that it is certainly made up of three segments.” He arrived at this conclusion through the homologizing of the setae and through JACKSON’s investigations (in 1890) on the pupae, which harmonized with the older (1875) observations of that writer on the so-called cremaster of the pupae, proving it to be the same as the anal-flap of the caterpillars. POULTON’s conclusion is l. c. p. 195: „In the pupa, this ninth abdominal segment, although small, is as distinct as any of the others. The part behind this segment in the larva forms a tenth abdominal segment. This segment is separated into a dorsal portion (X<sup>1</sup>) of which the posterior and lower part form the anal-flap and a ventral portion (X), of which the anal claspers form the posterior and lower part, between the latter is the anus”. On p. 196 he says that for a long time he has considered that X consisted of two segments.

SPULER (1910) also believes he can discern a 14<sup>th</sup> segment. fig. 4, p. XXVII. The last three segments he takes together as the anal segments. They often bear an „After-klappe”. „That the last part should be looked upon as the dorsal part of a 14<sup>th</sup> ring, consequently of the 11<sup>th</sup> abdominal segment, is proved by the

warts, but we cannot make out by the aid of the warts whether the lobes at the back of the XIII<sup>th</sup> segment which are separated by an incision, are to be considered as remnants of the ventral part of a XIV<sup>th</sup> segment, because the regular succession of the legless rings on the ventral side has been interrupted by the back feet."

SHARP (1901) however says on II p. 323: "The caterpillar is composed of a head and thirteen divisions or segments of the body, the first three of the latter are called thoracic, the other ten abdominal segments, in most caterpillars the terminal two or three abdominal segments are more or less run together, and the ninth may be very small, so that the true number is indistinct." Thus he leaves this highly important question of the number of primary segments unsolved.

J. TH. OUDEMANS thinks (1897—1900, p. 63) that the number of the abdominal segments is ten and that those who take it to be eleven are wrong.

FRACKER (1915) says of a full-grown *Hepialus* (p. 29): "We may consequently conclude that the setae give no evidence for considering the anal segment to be composed of more than one metamere either in its dorsal or ventral portions. Those who have asserted that the setae show that this segment consists of more than one somite, have not studied the data carefully on which their opinions were based."

Against this we may say that FRACKER does not speak of the arrangement on the newly hatched larva and that as early as 1886 MÜLLER observed that the first instar only showed this last segment distinctly, whilst at the same time we may contend that features, holding good for a certain form, may prove to be fallacious for another.

HANDLIRSCH (1903) on the basis of morphological, embryological and especially palaeontological investigations, came to the conclusion that insects, except the Collembola, possess eleven abdominal segments and a telson. In all the primitive insects this 11<sup>th</sup> segment ends in two cerci.

Neither do writers agree on the primary number of abdominal

legs (pedes spurii). Some of them, in imitation of KOWALEWSKY (1871) and TICHOMIROFF (1879) seek to provide all the abdominal segments with them. This conception is supported by embryology and comparative morphology. On the other hand DEGENER (1909, p. 3) considers these pedes spurii to be „secondary, adaptive, provisorial organs”. With a view to this controversy it is worth while to point out how, as early as 1886, MÜLLER called attention to the primary seta N<sup>o</sup>. 6, which occurs on the legless segments, but which is absent on the segments 6, 7, 8 and 9 (= abdominal 3, 4, 5 and 6).

FRACKER who has a different conception of these setae, does not go into this question at all. We see therefore that there are many different opinions on the number of the abdominal segments and on the question whether the abdominal legs are primitive or not. I think that I have adduced some proofs in Chapter VI of the presence of more than ten abdominal segments, and I believe that the regular presence of the seta pedalis also on those segments which bear no legs, should be taken as a proof that originally all the abdominal segments were provided with legs. This conception is also supported by embryology.

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## CHAPTER V.

### NOMENCLATURE AND PRIMITIVE PATTERN.

With a view to making the descriptions as clear as possible it is desirable to introduce a well defined nomenclature. WEISMANN (in 1876) made a first attempt, but as I pointed out in chapter II, he considered the setae of no importance and only gave names to the stripes.

SCHRÖDER also confined himself to these in his study on the *Geometridae* (1894). He found the same stripes as WEISMANN on the *Sphingidae* but in larger number. For the intermediate stripes, he introduced particular names which, however, can be brought back to WEISMANN's nomenclature.

W. MÜLLER (in 1886) gave a very useful terminology which also stands in connection with that of WEISMANN. He distinguishes the following „primary bristles” (see Pl. I, fig. 1, 2, 3. after W. MÜLLER).

On an abdominal segment.

1. on the back, next to the dorsal line.
2. a little ventrad and caudad of 1.
3. above the stigma.
4. behind the stigma.
5. under the stigma.
6. where we would expect the leg on the legless segments.

On the thorax:

1, 5, 6 as on the abdomen; 3 and 4 blended into one, 2 is wanting.

The spines have names and are called after the stripes along their base. The dorsal line can be single or double. He distinguishes:

*Dorsalia* (*D. s.*) viz. *D. s. ant.* if they are situated in front of, and *D. s. post.*, if they are lying behind the connecting line between the right and left subdorsal.

*Subdorsalia* (*S. d. s.*) the spines which are situated half way between the dorsalia and the stigma.

*Suprastigmalia* (*Sst.*) and *Infrastigmalia* (*Ifst.*) are determined by the situation of the stigma.

*Pedalia* under the infrastigmalia.

Though MÜLLER makes a distinction between the spines of the *Saturnidae* which arise from the primary setae and those of the *Nymphalidae* which do not come from those setae, he thinks (l. c. p. 246) that the names given in the first case may be kept.

SCUDDER (1889) did not give names to the setae but only to the stripes (see chapter II).

Independently of MÜLLER, DYAR proposed a new nomenclature in 1894, in which he purposely neglected the first instar, as it is „a generalized condition of tubercles and setae”, and it is not at all certain „that the character of presence or absence of this generalized first stage has any special phylogenetic significance” (l. c. p. 196).

He distinguishes two types: 1<sup>o</sup>. *Hepialus*. „This type consists (abdom. segm.) of five tubereles above the spiracle on each side, three in a transverse row about the middle of the segment and two behind, below the spiracle are two oblique rows, containing respectively two and four tubereles (l.c. fig. 2 p. 197. See Pl. I, fig. 4). 2<sup>o</sup>. The second type contains two dissimilar lines of modification of the first type. The fundamental arrangement is as follows: On each side above the spiracle three tubercles, below or behind the spiracle and above the base of the leg three more, on the base of the leg three (or four) on the outside and one on the inside near the midventral line. I propose to designate thus, counting from the dorsal line down the side: Tubereles I, II, III above the spiracle, IV, V, VI below it, the group of three on the outside of the leg as VII and the single one on the inside of the leg as VIII. VII and VIII are also present on the legless abdominal segments in the corresponding position” (l. c. p. 196—197, fig. 5, p. 198. See Pl. I, fig. 5).

In the *Psychidae* the three tubercles are retained on the middle annulet, while both are lost on the posterior one (l. c. p. 198, fig. 3). See Pl. I, fig. 6.

Other deviations also occur so that he separates the *Psychidae* from all the rest of the *Frenatae*.

The thoracic segments differ a great deal, the *Ia*+*b* and *Ila*+*b* occurring there, are not homologous with the abdominal *I* and *II* but they are simply called thus, because there often occur two tubercles, one above the other, each bearing two setae.

In 1901 DYAR came to different conclusions, especially through O. HOFMANN's criticism. He accepted HOFMANN's opinion about the homology of the thoracic setae.

O. HOFMANN (1898) found that in the *Pterophoridae* the prothorax deviates strongly from the rest. During instar *I* the mesothorax and the metathorax bear six setae and so does the abdomen. They are homologous but not in the way DYAR thought. A better homology runs thus:

DYAR            Ia, Ib, IIa, IIb, III, IV, V, and VI.

O. HOFMANN I, II, III, IV,            V,            and VI.

HOFMANN considers the setae called by DYAR III and V to be secondary or subprimary ones.

The setae I—IV are usually arranged more or less in a straight line. On Pl. I, fig. 8 I have indicated the place of the secondary setae by an \*, in O. HOFMANN's figure of *Taenioampa gothica* L. (l. c. fig. 2, p. 129).

From a comparison of fig. 7 and 8 we see what a confusion of numbers has been produced here.

In BEUTENMULLER's monograph on the *Sesiidae* (1900), DYAR described the caterpillars and here still used his old system. In the many descriptions, given by DYAR, attention must always be paid to the year of publication. In 1901 he proposed to call III and V on the thorax, which HOFMANN considered to be secondary setae, *Va* and *Vb* (these notations I have also used in fig. 8), whereby at the same time VI of the abdomen became *Vb* and VII became VI.

QUAIL (1900) usually speaks of DYAR's setae I and II as *trapezoidal tubercles*, in the same way as HOFMANN had done before. For the rest he uses names for the setae: supraspiracular, subspiracular, basal setae. For his description of the *Hepialidae* see chapter VI. In 1904 he laid stress on the study of the first larval stage. In that year QUAIL described the first instar of *Cossus cossus* and compared it with *Zeuzera pyrina*. Mr. A. BACOT pointed out to him „a minute free spiracular point of very general occurrence on the abdominal segments of lepidopterous larvae" (l. c. p. 95). QUAIL believes this point to be III B and he sees here already „that the elimination of spiracles probably is the chief cause of the altered positions of the tubercles on thoracic segments". In a second article of the same year (1904b) QUAIL comes to the conclusion, that II B (of DYAR) on the thorax is not similar to IV on the abdomen, as DYAR and HOFMANN take it to be, but that „the homologue of II B of the thorax is a minute anterior supraspiracular tubercle of the abdomen called by me

III B, that DYAR's III of the thorax is the homologue of a subspiracular tubercle of the abdomen and so on".

His terminology is best understood from the fig. 9 and 10, which are drawn after QUAIL's fig. 1, 2, 3, 4, Pl. IX 1904b.

We see that the confusion between the different writers becomes worse.

FORBES (1910) wrote a study which unfortunately I was not able to read. According to FRACKER (1915 p. 14), „he did not cover the subject of the homotypy of the setae. The few figures he labels, include errors for which he was not responsible, as he had not given the subject consideration" and (p. 35) „most of these associations would be very difficult to explain and they are wholly unnecessary. The mistakes (confusion of primary and subprimary setae) are due, not to errors in observation but to a failure to take the primitive first stage into account." In the table on p. 40 FRACKER says that the setae are named by FORBES in about the same way as I have done in fig. 11 and 12 of my Pl. I in accordance with his indications. It should be observed that the labelling of the Jugatae slightly differs in the numbers 4—6 viz:

<i>Frenatae</i> . . . . .	absent	IV	V	VI
<i>Jugatae</i> . . . . .	IV	V	VI	absent
according to FRACKER	♂	<i>x</i>	<i>γ</i>	<i>μ</i>

By his studies of the pattern of the pupa and imago, J. F. VAN BEMMELEN (1889, 1912, 1913, 1914, 1915, 1916) was led to an examination of the pigment spots of the caterpillars. In 1912 l. c. p. 115 he gives a synopsis of the spots on *Pieris brassicae*, larva pupa, and imago and of the pupa of *Aporia crataegi*. Following WEISMANN and W. MÜLLER he calls the spots after the rows in which they lie. He distinguishes: the dorsal, dorsolateral, epistigmal, stigmal, hypostigmal, ventrolateral and ventral rows. The first and the last are median, the others are paired. The number of spots in each row is either one, two or three, a group may replace one single spot. By the blending of the spots occurring on consecutive segments, stripes are brought about. See Pl. I, fig. 13.

As „stigma” originally is a greek word, much is to be said in favour of using the prepositions epi- and hypo-, instead of supra-, sub- or infra-. In connection however with the other terms and with the existing names used by WEISMANN and MÜLLER, I think that the words suprastigmal and infrastigmal might be retained. For the connection found by VAN BEMMELEN between the pattern of the pupa and that of the larva see chapter I and VII.

Tsou (1914) has a very peculiar way of indicating the setae.

His groups are: A = anterior, D = dorsal, S = subdorsal, C = circumstigmatal, L = lateroventral, P = pseudopodal, M = midventral. Each individual seta of a group is numbered as D<sub>1</sub>, P<sub>4</sub> etc. The setae belonging to the above groups are regarded as primary setae.

In chapter II, I have already expressed my objections to his method. For the sake of completeness I have copied on Pl. I, fig. 14 Tsou's figures of *Hepialus humuli*, the metathorax and the first abdominal segment (l. c. Pl. X, fig. 1 c. d.).

FRACKER (1915) has examined the setae of the caterpillars on a large scale. As appears from the synopsis given, the confusion in the numbering of the setae had become very serious. FRACKER has therefore rightly felt that he could not once more propose a new indication with the use of numbers. He began to pay attention to a certain segment and tried to find out in how far the same setae occurred on the same segment of the members of other families of the suborder. This he calls homology. In the second place he tried to compare the different segments of one caterpillar with each other and this he calls homotypy.

The use of this term might give rise to confusion.

In the widely spread „Lehrbuch der Zoologie von CLAUS-GROBBEN” 2<sup>nd</sup> edition (1910, on p. 12) is given:

*Homologous*: = morphologically equivalent.

*Homodynamous* = homologous organs, which repeat themselves in the longitudinal axis of the animal (e. g. vertebrae, pairs of legs of the Arthropoda etc.).

*Homotypical* = homologous organs which form the reflected images of each other, hence antimers; e. g. the right and left hands and the rays of a star-fish.

FRACKER therefore considers as homotypical what CLAUS-GROBBEN calls homodynamous. He arrives at the following definition l. c. p. 15: „Two organs on different segments of the same animal are homotypic, regardless of their positions at the present time, when they have developed from homotypic organs of a generalized ancestor. In a generalized type two similar organs on different segments are homotypes, when they bear the same relations to the other organs of their respective segments”.

On the whole I agree with this definition, but I wish to point out the hypothetic element which is hidden in it. It will often be difficult to tell how a certain seta is placed in a generalized ancestral type, so that in most cases it will be better to trust the second part of the definition rather than the first. Here we meet with a great number of difficulties, which FRACKER places under three headings:

1. Absence of intermediate stages between radically different conditions.

2. The lack of developmental series.

3. Apparently a lepidopterous larva has three or more entirely distinct types of arrangement of the setae (prothoracic, thoracic, abdominal, anal).

FRACKER obviates these difficulties in the following manner, l. c. p. 17: “The setae of the prothorax, metathorax and abdomen of the generalized members of both sub-orders of Lepidoptera were plotted, one segment over the other, as if all were on the same segment. The number was about fifteen (fig. 1) and they were in approximately the same position as on the prothorax of the most generalized forms of the order.” (in casu *Hepialus mustelinus*). These primary setae FRACKER indicates by the characters of the Greek alphabet, p. 23, because:

1. A special letter can be introduced for a subprimary seta in a limited group without disarranging the system.

2. The alphabetical order is not so fixed in the mind as to prejudice one in regard to homology.

He distinguishes:

*Primary* setae on the newly hatched larvae.

*Subprimary*, appearing after one moult, but fairly constant ( $\mu, \vartheta$ ).

*Secondary*, no constant position but scattered, very rare in the first instar.

Pl. I fig. 15 shows FRACKER's indication best.

The above-mentioned writer thinks it justifiable to conclude from the setae on the prothorax of the *Tortricidae* (l. c. fig. 39), *Aegeriidae* and *Yponomeutidae* (l. c. fig. 35), that  $\varepsilon$  remains in its place and  $\rho$  moves forward towards it, whilst in the Macrolepidoptera the opposite movement is to be noted. In the latter  $\varepsilon$  has migrated back to  $\rho$  on the fullgrown larva, whilst they are far away from each other on the newly hatched larva (l. c. p. 34).

He therefore thinks that, for instance, in instar I the first seta over the stigma of *Feltia glandaria*, is not  $\gamma$  or  $\varepsilon$  but  $\rho$  (see Pl. I, fig. 17).

On the mesothorax and the metathorax also he arrives at conclusions, which differ from those of former writers.

These differences have been expressed in his figures, which are kept very diagrammatic. Seta  $\rho$  as well as seta  $\beta$  is always turned caudally, whilst  $\alpha$  and  $\varepsilon$  point in an oral direction. These figures already suggest the hypothesis proposed by FRACKER. For the formation of an unprejudiced opinion it is therefore preferable to pay exclusive attention to the points of implantation of the setae on the skin.

I also wish to draw attention to Pl. I, fig. 16 which agrees with FRACKER's Pl. V fig. 36, the mesothorax of *Atteva aurea* (*Yponomeutidae*).

FRACKER sometimes unites the setae into several groups:

$B = \alpha + \beta$ .  $K = \vartheta + \alpha + \gamma$ .  $P = \varepsilon + \rho$ .

$\Pi = \nu + \pi$  (on thorax),  $\nu + \pi + \tau$  (on abdomen).

$T = \tau + \phi + \omega$ .

Before proceeding to the nomenclatures I should like to

propose and which I have used in the following descriptions, I have to subject to criticism the systems which have been so far used.

Concerning the indication of the setae by means of cyphers, as used by W. MÜLLER (1886), DYAR (1894 and 1901), QUAIL (1904 and 1904 *b*), FORBES (1911), these writers have made so many changes, that it would be a hopeless task to try to improve it.

FRACKER has grouped together the opinions of the different investigators into a table (l. c. p. 40). For a single slight modification I wish to quote a striking case from it. QUAIL indicates the large seta over the stigma with III or IIIA and the small one in front of it with IIIB, and not as FRACKER does: with III and IIIA respectively. If we look at the seta over the stigma on the abdomen, we see that it has been named in the following ways:

*Mesothorax and Metathorax (Frenatae).*

MÜLLER 1886,	DYAR 1895,	HOFMANN 1898,	DYAR 1901,	QUAIL 1904,	FORBES 1910.
4.	IIb.	IV.	IV.	III.	II B.

*Abdomen.*

MÜLLER 1886,	DYAR 1895,	HOFMANN 1898,	DYAR 1901,	QUAIL 1904,	FORBES 1910.
3.	III.	III.	III.	III A.	III.

So, whilst on the abdomen at least all the writers have given the same cypher to this seta, FRACKER considers it to be  $\rho$ , to which in *Hepialus* the others certainly would not have given this index, as  $\rho$  belongs to the caudal row, and the abdominal seta III has been placed by the majority of writers in the oral row. Anyone can find other examples from the figures placed side by side on Pl. I.

Tsou's system I have already discussed. Of the systems in which no names are used, that of FRACKER is the most important, and against this system I have serious objections.

In the first place FRACKER's method of concentrating all the setae occurring on the several segments of different larvae into one segment and of declaring this hypothetical segment to be the original form, is wrong.

For it is probable that a certain organ of a given original

form gets specialized in very different directions and in so doing gives rise to numerous new forms, one group acquiring this, another group that improvement.

In a case like this, that organ is the most primitive which does not show any new modifications, hence has preserved the characteristics which they have all in common in the pure forms, but certainly not such an organ, as we might artificially compose by summarizing all the new formations.

It is my opinion that this way of looking at the question can be justified equally well, and that it is certainly oftener used in comparative anatomy than the method of FRACKER, of which he asserts that it is the ordinary one in problems of this kind (l. c. p. 17).

FRACKER tries to give a solid basis to this summarizing hypothesis by the description of the prothorax of *Hepialus lupulinus*. In the first place the drawing on which this description has been founded is not FRACKER's but DYAR's work. And though I have a great respect for the exactness with which this writer generally works, it still remains exceedingly dangerous to take another man's drawing like this, as the chief basis of a hypothesis which upsets all former ideas. This, however, is not the greatest objection which I have to FRACKER's opinions. The point I am going to treat now is of a more general nature.

I think that it is not quite scientific to raise one segment, picked out at random in an arbitrarily chosen family, to the rank of the most generalized type. Such a procedure could only be justified by adducing a number of facts to prove that all or at least nearly all the members of the family possess the same foundation. This is not at all the case here and QUAIL's descriptions of the *Hepialidae* (1900) might have taught FRACKER (1915) as much. Though the family of the *Hepialidae* is justly considered to be a primitive one, this does not include the necessity that all the features of all the members have to show a primitive character and that they cannot possibly have undergone any secondary modifications. A study of the existing literature would have taught FRACKER that in 1914 and 1915 (and in 1916), J. F. VAN BEMMELEN found

very primitive qualities in the pattern of the wings of the *Hepialidae*, but nevertheless could show at the same time great secondary alterations in it.

It does not seem advisable to me to look upon the pattern of one segment of one single representative, as the generalized type of the Jugatae, from which the generalized type of the Frenatae has descended. And this applies in a high degree to the prothorax.

In a preceding chapter I think, I have proved sufficiently that the thorax on the whole is not built primitively, that the stigmata on its surface have been shifted and that the wing-rudiments very soon bring about changes in these segments.

By nearly all the writers the prothoracic stigma is considered to have been shifted towards the oral side and it is strange to choose this very segment as a starting-point.

It seems to me a very *unfortunate* accident that the setae on the prothorax of *Hepialus lupulinus* (l. c. p. 17) are also about fifteen and that they were in approximately (!) the same position as on the hypothetical segment.

Another objection I have to FRACKER's assertion is, that  $x$  and  $\mathcal{S}$  on the prothorax should be homologous with  $x$  and  $\mathcal{S}$  of the abdomen (c.f. on this point my Pl. I, fig. 15).

On the prothorax we find these setae in front of the stigma, on the abdomen behind it, without there being any change in the position in regard to the other setae. There we get the impression as if the stigma had passed under these setae, a kind of dislocation, the possibility of which I cannot understand. I am convinced that a seta which is situated in front of the stigma must remain prostigmal, and that it will either disappear in case the stigma is shifted, or that it will display the traces of the shifting of the stigma in its situation on the segment. Therefore I think that the seta called III B by QUAIL may agree with a prostigmal seta, even if this seta is sometimes placed a little higher.

The "proofs" mentioned by FRACKER of the shifting of  $\epsilon$  and  $\rho$  do not appear to me to be convincing. The upshot of these arguments is always the preconceived idea, that we must consider

the thoracic segments in general and the prothoracic one in particular, to bear a primary character. I think I have shown sufficiently in chapter III that this a-priori view does not deserve general acceptance.

In criticizing the different systems and especially that of FRACKER, I have had the opportunity of explaining my opinion on the nomenclature.

Therefore it will not cause surprise that I begin by first taking the abdominal pattern and that, as neither the use of numbers nor of FRACKER's Greek letters appeared possible, I have come back to the use of names which at the same time express the place of the seta on the segment. In composing my nomenclature I have tried to keep in agreement as far as possible with the following writers:

WEISMANN (1876), MÜLLER (1886), SCUDDER (1889), SCHRÖDER (1894), QUAIL (1900), J. F. VAN BEMMELN (1912).

In accordance with DYAR and FRACKER I think that in the composition of a primitive pattern a *verruca* (wart), a *scelus* (spine), a *tuberculum* (elevation which mostly bears one or more setae) and a *seta* ought to be considered homologous with each other.

I should like to add to this series of homologous organs a *pigmental spot*. I think that the *seta* is the original part, and that the other organs are its secondary modifications. A homogeneous spreading of the setae, as also their complete absence, must be considered as secondary features.

The reduced patterns of the anal segments have also arisen in a secondary way, though they often lead to pseudo-primitive conditions.

In discussing the results I intend to refer again to these facts (chapter IX).

To be able to shorten the descriptions I have also given cyphers to the patterns as a whole: Type I, Ia etc. The deviations from this pattern can be easily indicated so that with a few words the place of all the setae can be exactly mentioned. In connection with my remarks in Chapter IV it should be pointed out, that the anal

segments deserve special mentioning. For them I cannot give any definite rules, as in some cases they are far more reduced than in others.

**Type I.** This pattern consists of the following setae, tubercula etc. (Pl. I, fig. 19).

*Seta dorsalis* on the oral and at the same time on the dorsal edge of the segment.

*S. subdorsalis superior* more caudal and also a little more ventral than the former.

*S. suprastigmatis* lying over the stigma, about in a line with the stigma and *s. dorsalis*.

*S. prostigmatis* is usually very short and stands right in front of the stigma or has been shifted a little upwards.

*S. poststigmatis* caudal and in most cases somewhat ventral of the stigma.

*S. infrastigmatis* under the stigma.

*S. basalis anterior* and

*S. basalis posterior* situated between *s. infrastigmatis* and the place where the leg is implanted, or where this is wanting, between *s. infrastigmatis* and *s. pedalis*.

*S. pedalis* at the beginning of the leg and, if the leg is wanting, on the place where we might expect it.

In connection with the remarks in chapter IV the presence of this seta seems to me a proof of the secondary disappearance of the legs on the abdominal segments 1, 2, 7, 8, 9.

*S. propedalis* on the ventral side, in front of the beginning of the leg.

*S. ventralis* between the inner side of the leg and the ventral median line.

We see that this Type I almost completely agrees with the pattern chosen as the fundamental plan by W. MÜLLER (1886), DYAR (1894), O. HOFMANN (1898) and QUAIL (1904). Where, in my investigation independently of them, I was led to the same type, I think I am justified in attaching great value to this result.

As rather frequently occurring extensions of this type, there also occur:

*S. subdorsalis inferior* lying ventral of *s. subdorsalis superior*.

*S. dorsolateralis* implanted on the oral edge of the segment between *s. dorsalis* and *s. suprastigmatis*.

In the descriptions I think it better to mention, whether these setae are present or not, whilst I consider it advisable to make a special notice of *s. prostigmatis* and *s. propedalis* as they often show important deviations in size.

**Type Ia.** A simplification of frequent occurrence is that the *seta subdorsalis* disappears, whilst *seta poststigmatis* is united with *seta infrastigmatis*.

Consequently we get one series in which the stigma is also situated. This pattern, which at first sight makes a primitive impression, is found i. a. in *Saturnia pavonia*. The setae have already changed in instar *I* into *verrucae*, later on in *scoli*, but one *seta dorsalis* remains on the prothorax as a proof that here as everywhere else the *verrucae* have arisen by modification of the setae (c. f. Pl. I, fig. 20).

**Type Ib.** At the end of larval life the conditions of the pattern are nearly the same in the *Lymantridae* = *Liparidae*. Here however *verruca subdorsalis* does not disappear, but *verruca dorsalis* does, whilst *v. poststigmatis* is blended with *v. suprastigmatis* and not with *v. infrastigmatis*. This pattern I call type *Ib*.

Apparently the types *Ia* and *Ib* are almost alike, in reality they have arisen independently of each other.

The coalescence of *v. poststigmatis* and *v. infrastigmatis* remains during all the larval instars and even in the pupa it is represented by a furrow which separates the two halves from each other (Pl. I, fig. 21).

**Type II.** At first sight the meso- and the metathorax seem to possess a setal pattern which is entirely different from that of the abdominal segments (Pl. I, fig. 18).

They agree, however, so much with the prothorax, that it does not seem advisable to establish a special type for it but to describe it as: type **I** without seta . . . . or: type **II** with seta . . . . ., etc.

The opinions of the investigators differ very much on the meso- and the metathorax, as may be seen from FRACKER's list (1915 l. c. p. 40), from the figures arranged by me on plate I and from the example on page 38.

I think that the cause of the difference between type II and type I must be sought in the shifting of the stigmata and in their final disappearance later on.

On the meso- and the metathorax one generally finds three setae at the oral border of the segment, mostly arranged in one vertical line.

About in the same row, but sometimes a little in front of it or behind it, is another seta, and behind this one we often find a peculiarity of the surface of the skin. Sometimes in the shape of a pigmental spot (e.g. *Porthesia chrysoorrhoea*, *Zeuzera pyrina*), another time in that of a verruca (e. g. *Arctia caja*, *Sericinus telamon*), or as a distinct dilatation of the system of air-tubes, which is seen through the transparent skin (e. g. *Pieris brassicae* and *P. napi*). These variations of the surface of the skin I take to be caused by the wing-rudiment (BOAS 1899), but, as it is situated on the place originally occupied by the stigma, the seta which is placed in front of it keeps its character as *s. prostigmalis*. On this point I agree with QUAIL, who calls it III B. Under this seta stands another one, and over the base of the leg, one more. All these six setae are situated in one vertical row. This type seems therefore to be very primitive. But having seen that type Ia and Ib are pseudo-primitive and after having explained in chapter IV that the thorax is generally of a secondary construction, I think another point of view may also be taken.

The uppermost seta does not give any difficulties, and may safely be considered to be *s. dorsalis*, and the fourth *s. prostigmalis*. In this case it is clear, that the two last setae are *s. infrastigmalis* and *s. basalis* and that the third of the row is *s. suprastigmalis*. There remains still one seta, namely the second of the row.

It can be easily understood that this seta is considered by many

investigators to be *s. subdorsalis*, removed to the front-border of the segment. But against this explanation I have an objection for the following reasons :

1°. In different families there appear on the abdomen three setae above the stigma: e. g. *Phalera bucephala*, *Hepialus*, *Pieris napi* and the *Psychidae*.

2°. On the prothorax we very regularly find *s. dorsolateralis* together with *s. subdorsalis*.

3°. On all the pupae of Rhopalocera, which I have examined and which possess a pattern, I could show three elevations or pigment-spots on the oral side of the abdominal segments, above the stigma. At the same time there exists a spot or an elevation, agreeing with *s. subdorsalis*.

In all three cases it is evident, that the middle one of the three setae is not *s. subdorsalis*. This seta I have called *s. dorsolateralis*.

At first I hesitated whether we could possibly explain this seta in another way, namely by calling the upper one *s. dorsalis*, the next one *s. suprastigmalis* and by considering the third one as agreeing with III B of QUAIL. I thought at first that III B had changed its place and had come above the stigma and by this transgression had caused a dorsad motion of *s. suprastigmalis*. I think, however, that the seta before and not that above the transparent wing-rudiment, viz. *s. prostigmalis*, agrees with III B.

A third possible explanation of the thoracic arrangement follows here:

Starting from the idea that the prothoracic stigma really belongs to the praesegmental zone of the mesothorax, and that the metathoracic stigma is removed to the intersegmental membrane, it is easy to imagine, that the setae lying in the neighbourhood have also taken part in this shifting. Further taking it for granted that the setae on the thorax are originally arranged in the same way as on the abdomen, we also find there *s. suprastigmalis*, *s. prostigmalis* (III B), *s. poststigmalis* and *s. infrastigmalis*. If a stigma is shifted from the oral side of a segment to the caudal

edge of the former, then *s. poststigmalis* becomes prostigmal in respect to this stigma.

In that case there must exist two *s. prostigmales*. If *s. infrastigmalis* also takes part in this shifting, there are three *s. prostigmales*. This then would agree with FRACKER's bisetose and trisetose K.-group.

On the mesothorax and the metathorax *s. poststigmalis* can be removed so much, that it comes in one vertical line with *s. suprastigmalis*.

It is easy to imagine, that hereby *s. prostigmalis* is pushed upwards and thus occupies the place of *s. suprastigmalis*. This one is also shifted and appears between its old place and *s. dorsalis*, i. e. on the place of *s. dorsolateralis*.

It is also possible that *s. infrastigmalis* is removed downwards and so appears on the place of *s. basalis*. I think that this explanation is very artificial, but still it seems to me better than that given by FRACKER. That a stigma can be shifted in such a manner that it plunges under the setae, without exerting any influence on their position, seems to me highly improbable. I think however that the cases mentioned sub 1, 2 and 3 form an argument against this explanation, which is given here for the sake of completeness only.

Besides it seems to me entirely incorrect to introduce in a nomenclature hypothetic views on homology. In human anatomy we might as well call the muscles and bones of the arm and legs by the same names, if they were considered homologous for some more or less probable reason. In my opinion a nomenclature ought to be a means for a short and clear description and it should not be the expression of hypotheses on which various investigators have different opinions. Through this, it is made difficult for outsiders to understand the terminology, and the investigators of the setal pattern themselves will, each with the same right, claim their own hypothesis to be the right one.

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## CHAPTER VI.

## SYSTEMATIC SYNOPSIS OF THE SETAL PATTERN OF CATERPILLARS.

Not much harmony is to be found in the classification of the Lepidoptera. Some of the latter-day writers reject the sub-order of the Jugatae, but even if this sub-order is accepted, the sub-order of the Frenatae remains an extraordinarily difficult problem for the systematists.

The principal newer systems are:

CHAPMAN (1893), especially founded on the pupae.

COMSTOCK (1893), especially founded on the wing-venation.

DYAR (1894 and 1894*b*), especially based on the setal pattern of caterpillars.

PACKARD (1895), starts from the three preceding systems and the geographical distribution.

SPULER (1895 and 1910), especially founded on the wing-venation.

HANDLIRSCH (1908), based on palaeontological data and on the preceding systems.

I have followed the last-mentioned writer, because he has worked into his system all the previous ones and because I think that the palaeontological data have been neglected too much by the entomologists. HANDLIRSCH's great knowledge of the morphology, embryology and palaeontology of the insects, makes him an authority deserving confidence. Therefore I have not followed SCHARP's manual, as I did in my preliminary note (1916).

As far as possible I have mentioned the literature with each family. It is more than possible that I have not noticed some of the very scattered articles in the entomological periodicals. I therefore wish to draw attention to the fact that owing to the war, I have not been able to procure some of the foreign periodicals. In the first sub-order I have explained the data known to me rather in detail, because in this way I hoped to assist in the solution of one of the most difficult problems in the systematic arrangement of Lepidoptera.

My work, however, would become too comprehensive if I had tried to do the same for all the families.

Sub-order I. *Jugatae*.Family I. *Eriocephalidae*.

In many respects this family is very primitive but with respect to the setae it is exceedingly specialized. I do not possess any material for investigations and am therefore obliged to confine myself to literature, especially to one article of CHAPMAN's (1894). It is a great pity that no more is known about these highly interesting larvae, which possess the full set of functioning abdominal legs (1—8) and give rise to imagines, which, as WALTER found in 1885 for *Micropteryx* (*Eriocephala* = *Eriocrania*) *calthella*, retain the mandibles as biting organs and the first pair of maxillaries fully developed.

DYAR (1893 and 1894*b*) does not give any characteristics.

CHAPMAN (1894) gives a very interesting description, with figures of the larva of *Micropteryx calthella* R. which has been checked and copied by PACKARD (1895) and which also occurs (with figure) in the manual of OUDEMANS (1900).

On the newly hatched larva there are ten rows of globular rough warts, each of them on a little stem. They are placed on four elevated ridges, and become smaller and smooth when the larva grows.

HANDLIRSCH (1908, p. 1254) says that there are several rows of tubercles on the back. Like the other writers, he draws attention to the abdominal legs at the segments 1—8.

FRACKER (1915) does not discuss this family.

Family II. *Micropterygidae*.

In the pupae of this family CHAPMAN (1893) discovered the gigantic mandibulae. Their larvae, on the other hand, are more secondarily modified, in so far as they lack the abdominal legs.

For want of material I could not study their setal pattern.

DYAR (1894*b*, p. 49) describes *Micropteryx purpurella*: "The arrangement of the setae corresponds with that of *Hepialus*, except that the four setae on the base of the leg are absent . . . . It has a double dorsal shield on every segment which may account for

the unusually posterior position of tubercle I (fig. 7 l. c. p. 49). The uniform position on the thoracic segments of the Frenatae is lacking." In my opinion the arrangement of the setae might equally well be conceived as follows: *s. dorsalis* absent, *s. suprastigmatis* or *s. dorsolateralis* on the oral side, *s. subdorsalis sup.* and *inf.* on the caudal side, *s. poststigmatis* and *s. infrastigmatis*, two *s. basales*.

PACKARD (1895, p. 62) does not mention the larvae of this family but draws a few setae on the nympha.

FRACKER (1915, p. 24) only says that the setae have been reduced so far by leaf-mining habits that conclusions cannot be based upon them.

### Family III. *Hepialidae*.

For this family which interested me especially in connection with the investigations of J. F. VAN BEMMELEN on the pattern of the wings (1912—1916), I had material of two species at my disposal.

DYAR (1894, p. 197) described *Hepialus lupulinus*, full-grown specimen and later on (1895, p. 66 sqq) instar I of *Hepialus mustelinus*.

DYAR especially emphasized the differences between the Jugatae and the Frenatae, and did not describe the prothorax.

PACKARD (1895) described *Hepialus mustelinus* instar I and full-grown larvae of *H. humuli* and *H. hectus*. These latter he figured together with the pupa of *Oncopora intricata* on p. 72 and 73 of the first part of his work on the Bombyces. I wish to draw special attention to these pictures, because FRACKER does not mention them. The prothorax of all three agrees much more with my description than with that of FRACKER, which has been selected as the fundamental scheme of the pattern of all caterpillars. *H. hectus* agrees best with it, but just this species is considered by PACKARD to be a specialized one.

QUAIL (1900, Pl. VI, fig. 11, 12, 13, 14) gives a description and a figure of the newly hatched larva of *Porina cervinata*

Walk. and of full-grown larvae of *P. umbracaluta* Gn. and *Charagia virescens* Dbld. He also describes the pupa of *Porina cervinata* Walk. and figures, moreover, the last segments with the setae, which are in the same position as on the caterpillar.

These descriptions too differ in important respects from FRACKER.

TSOU (1914) minutely describes: *Hepialus humuli* L. and gives the setal maps of many segments. This is the same kind which FRACKER examined, but TSOU draws a few more setae. Among other things he puts  $C_2$  on the prothorax on the shield, whilst FRACKER draws it as  $\mathcal{S}$  on the outside. On abdominal segment 1 he places  $S_1$  between  $\beta$  and  $\rho$  and in front of  $S_2$  ( $= \epsilon$ ) a special seta A.

FRACKER (1915) who considered the prothorax of *Hepialus mustelinus* as the primeval type of the pattern should, by a thorough study of the literature, have compared different descriptions and illustrations. I am convinced that the list of the drawings and descriptions of caterpillars of the Hepialids already cited by me, is far from complete. When a student attaches so much importance to a certain family, as FRACKER does, I think it only right, that he should make as far as possible a complete perusal of the existing literature and that he should not confine himself to one special type, which accidently proves to be suitable for a certain hypothesis. And the more so where the other Jugatae: the *Eriocephalidae* and *Micropterygidae* show so many deviations from this type. FRACKER himself described full-grown larvae of *H. humuli*, *H. hectus* and *H. lupulinus*. I have already discussed his investigations in the chapter on the nomenclature.

#### *Hepialus hectus* Linn.

Instar I. Length 1 mm. Duration? Material in alcohol, collected at Groningen 1914, from eggs, bought in Germany. Plate I, fig. 22, 23, 24.

The head of this caterpillar, the smallest, which I have examined, is relatively large, to wit more than  $\frac{1}{4}$  part of the length of the body. The upper-jaws are strongly developed. There are many

setae on the head which I drew with accuracy, but which I did not study further. The ocelli are arranged in two vertical rows, each containing the number of three, between which stands a seta. No distinct prothoracic shield. On each of the tubercula there is one seta which, on being magnified 400 times, still shows no plumes and which has a length of 50—150  $\mu$ .

The tubercula are not coloured.

*Prothorax.* *Seta dorsalis*, *s. subdorsalis sup.* and *inf.*, *s. dorsolateralis*, *s. prostigmalis*, *s. infrastigmalis*, *s. basalis*, *s. propedalis*, *s. ventralis*. On the leg several *s. pedales* and behind the leg on the ventral side a *s. postpedalis*, which only occurs on the thorax.

*Mesothorax.* *S. dorsalis* and *s. prostigmalis* on the oral edge of the segment. Behind these, approximately in a line, *s. subdorsalis sup.* and *inf.*, further *s. infrastigmalis*, *s. propedalis*, *s. basalis*, *s. postpedalis* and *s. ventralis*.

*Metathorax* = *mesothorax*.

*Abdomen 1.* *S. dorsalis*, *s. subdorsalis sup.* and *inf.*, *s. suprastigmalis*, *s. poststigmalis*, *s. infrastigmalis*, *s. basalis*, *s. pedalis* or *s. ventralis*.

*Segm. 2* = 1.

- " 3, 4, 5, 6 are as 1 and 2, but *s. poststigmalis* is situated a little lower down than usually; there are two *s. basales*, one *s. propedalis* and one *s. ventralis*.
- " 7, 8 = 1, but *s. basalis* lies a little higher.
- " 9. *S. dorsalis*, *s. subdorsalis sup.*, *s. suprastigmalis*, two *s. basales*, *s. propedalis*, *s. ventralis*.
- " 10. *S. dorsalis*, *s. subdorsalis sup.*, *s. suprastigmalis*, *s. propedalis* or *s. basalis*, *s. ventralis*.
- " 11. *S. dorsalis* and further on the caudal side of the prolegs two setae, in my opinion: *s. subdorsalis* and *s. suprastigmalis*; one *s. propedalis* and on the ventral side of the claspers one seta, in my opinion to be put on one line with *s. ventralis*.

I clearly see here an eleventh abdominal segment, whereas FRACKER in *H. mustelinus* only distinguishes ten.

*Hepialus spec. cf. lupulinus* L. Plate II, fig. 4.

*Material.* Through the kindness of Mr. CLAASSEN, Instructor of the Government Horticultural School at Boskoop, Prof. Dr. J. F. VAN BEMMELLEN procured material from the nurseries there. Some years they are so abundant, that they damage the roots of the lilacs, but in 1915 they were so scarce, that only a few specimens could be obtained. The smallest measured was 2 cm., the biggest 3 cm. (preserved in alcohol). Judging by the size of the head they seem to belong to the same instar. The head is flat, large, covered with setae. The ocelli are arranged in two vertical rows of three each, between which there is one seta. The upper-jaws are large. The setae of the body are placed on tubercula which are not coloured. The setae are 1000—2500  $\mu$ . long and not plumed.

*Prothorax.* This segment is almost completely hidden by the head. No prothoracic shield. Over the stigma there is only one seta, probably *s. subdorsalis*. Further there occur *s. infrastigmatis*, *s. poststigmatis*, *s. basalis* and on the leg many *s. pedales*.

*Mesothorax.* *S. dorsalis*, *s. dorsolateralis*, *s. subdorsalis superior*, *s. poststigmatis*, *s. infrastigmatis*, *s. basalis*, many *s. pedales*.

*Metathorax.* *S. dorsalis* and *s. dorsolateralis* between which there are still three other setae, which in all specimens occur on the metathorax, but not on the mesothorax; *s. suprastigmatis*, *s. subdorsalis sup.*, *s. poststigmatis*, *s. propedalis*, *s. basalis* and many smaller *s. pedales*.

*Abdomen 1.* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis*, of which the two last ones are close together and *s. dorsolateralis* is a little more oral, *s. subdorsalis sup.* and *inf.*, *s. poststigmatis*, two *s. infrastigmatis* of which the foremost might be compared with *s. prostigmatis*; *s. basalis*, *s. propedalis*, *s. pedalis* or *s. ventralis*. *Segm. 2 = 1*, but lacks *s. subdorsalis inf.*

" 3 = 2, but has mostly five *s. basales*.

" 4, 5, 6 = 3 but only three *s. basales*.

" 7 = 2.

" 8, stigma extraordinarily large, three *s. basales*, which are placed higher than usual.

- Segm. 9* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis* in one line, *s. subdorsalis sup.*, *s. poststigmatis*, two or three *s. infrastigmatis*, *s. basalis*, one *s. propedalis*.
- ” 10. *S. dorsalis* and *s. dorsolateralis* are wanting, *s. suprastigmatis*, *s. subdorsalis sup.*, *s. poststigmatis*, two *s. infrastigmatis*, *s. propedalis* and five or seven *s. pedales* with very long setae.
- ” 11. As there are no *s. pedales* on the abdominal legs I am inclined to ascribe the setae pedales of segment 10 to a reduced segment 11.

*Synopsis of the sub-order of the Jugatae.*

It is not possible to build up a pattern which they have in common, as each family certainly possesses its own pattern and it may be so with each genus. This may be expected as the Jugatae most probably are not the immediate ancestors of the Frenatae. Only in some respects they have preserved the primitive character of the Lepidopterous tribe in a better way. Where HANDLIRSCH (1908) places the separation of the Frenatae from the Jugatae as early as the Lias, because in Dogger and Malm the *Palaeotineidae* already belong to the Frenatae (l. c. p. 1253 sqq.), this result need not surprise us.

When the setae alone are concerned I would rather conclude that the *Eriocephalidae* descend from the *Micropterygidae* than the reverse, but I admit that a system, only based on the form and the number of the setae would be exceedingly artificial. Moreover there is a possibility, that in this respect the *Micropterygidae* have remained in a more primitive state, especially by their mining habits, instead of the *Eriocephalidae*, which are exposed to all kinds of exterior influences, by which the form of the setae might be highly modified. The *Eriocephalidae* are the most specialized forms in a progressive line, the *Micropterygidae* are perhaps reduced. The different *Hepialidae* deviate very much from each other, the prothorax is often highly reduced. It is of importance that a *s. dorsolateralis* and a *s. subdorsalis inf.* frequently occur.

With a good deal of probability 11 abdominal segments can be counted in instar *I* of *H. hectus*.

For these families I have collected as much literature as possible, and I think I am justified in my conclusion that FRACKER made a bad choice in raising the prothorax of one of the numerous species to the rank of a fundamental form for his generalized type.

### Sub-order II. **Frenatae.**

As it was FRACKER's (1915) intention to compose an analytic list of determinations of the caterpillars, he had to examine as many different families as possible. In some respects I have started from a different point of view and I had by no means such an extensive material at my disposal as he had. Though I am convinced that it will be advantageous for a good system of the Lepidoptera to be acquainted with the setal pattern of all the caterpillars, yet I do not believe that the setal pattern in itself is a reliable guide for the limitation of families etc. My own experiences of the *Sphingidae*, the *Hepialidae*, the *Cossidae*, as well as HOFMANN's observations of the *Pterophoridae* etc. have increased my doubts upon that point. This result which later on I intend to discuss more fully, added to my lacking complete series in many families, and on the other hand the numerous data given by DYAR, PACKARD, FRACKER and others, allowed me to confine my work to certain selected cases.

For those families which I have not examined I will confine myself to mentioning the literature I have collected, generally without entering into criticism.

The arrangement of the groups has been made according to HANDLIRSCH's plan (1908), but those families of the so-called Microlepidoptera, which he does not mention, I have entered into the series according to FRACKER's system. This is based on a compilation from WALSINGHAM and on published and unpublished work of AUGUST BUSCK (l. c. p. 48, 61 sqq.). As this system differs in many instances from that of HANDLIRSCH, I have

placed the families, not mentioned by him, next to those with which, according to FRACKER, they harmonize best.

Family *Nepticulidae*. FRACKER (1915, p. 64) does not state anything about the setal pattern, neither does WOOD (1894).

Family *Prodoxidae*. FRACKER (1915, p. 64) does not say anything of the setal pattern.

Family *Incurvariidae*. FRACKER (1915, p. 65) does not mention the setal pattern. PACKARD (1895, p. 63, fig. 7) describes *Adela viridella* and *Nematois violellus*. The setal pattern is not distinct, but differs much in the two kinds mentioned.

Family *Tischeriidae*. FRACKER (1915, p. 66) does not say anything of the setal pattern. These last four families are taken together as the *Aculeata*.

Family *Acrolophidae*. FRACKER (1915, fig. 7, 8; I, II; 1, 2, 3; p. 66) *Pseudanaphora arcanelle*. The abdomen bears: *s. dorsalis* ( $\alpha$ ), *s. subdorsalis* ( $\beta$ ), *s. suprastigmatis* ( $\gamma$ ) *s. prostigmatis* ( $\epsilon$ ), two *s. infrastigmatis* of which the hindermost may agree with *s. poststigmatis*; *s. basalis*, three *s. pedales*, *s. ventralis*.

Family *Tineidae*. QUAIL (1904b, Pl. IX) gives a figure of *Tinea pellionella*. There is an extraordinarily small *s. prostigmatis* and under the stigma two *s. infrastigmatis* in one vertical line.

FRACKER (1915, p. 67) says that the *s. dorsales* ( $\alpha$ ) are further from each other than the *s. subdorsales* ( $\beta$ ). It may therefore be possible, that here his  $\alpha$  agrees with *s. dorsolateralis*.

Family *Buccalatrigenidae*. FRACKER (1915, p. 67) says the same of the segments 8 and 9 as of the *Tineidae*, further are  $\alpha$  and  $\gamma$  widely separated, thereby corresponding with *s. infrastigmatis* and *s. poststigmatis*.

Family *Lyonetiidae*. FRACKER (1915, p. 67) gives a statement of the pattern but he himself does not attach much value to it.

Family *Helioniidae*. FRACKER (1915, p. 68) says only that *s. poststigmatis* and *s. infrastigmatis* are placed in different ways on the body of the genera examined. *Lithariopteryx abrioniaella* carries them on different tubercles, *Antispila nyssaefoliella* on the same tubercle.

Family *Yponomeutidae*. FRACKER (1915, p. 69) mentions a great difference between the several genera, the only characteristic in common being (and even this does not always hold good) that *s. subdorsalis* ( $\beta$ ) is lower on the prothorax than *s. dorsalis* ( $\alpha$ ), that the K. group (*s. prostiginales* and *s. infrastiginales*) consists of three setae on the prothorax, and that on the abdomen *s. poststigmalis* and *s. infrastigmalis* are separate from each other.

Family *Gracilaridae*. FRACKER (1915, p. 70) does not give a setal pattern, neither does CHAPMAN (1902).

Family *Tortricidae*. FRACKER (1915, p. 71—74) gives a summary of the genera, which differ very much from each other. Moreover the characteristics are not absolutely constant. Changes occur with the following setae:  $\Pi$ ;  $\delta$ ,  $\beta$ ,  $\kappa$ ,  $\gamma$ ,  $\mu$ , K. It is of importance that  $\kappa$  and  $\gamma$ , i. e. *s. poststigmalis* and *s. infrastigmalis*, may be arranged on the abdomen in a horizontal line as well as in a vertical line and that  $\epsilon$ , i. e. *s. prostigmalis* is placed on one tubercle with *s. suprastigmalis* ( $\rho$ ).

#### Family *Cossidae*.

Material: Only a certain number of full-grown specimens of *Cossus cossus* L. (*ligniperda*) were at my disposal.

*Zeuzera pyrina* L. from the Coll. Kall.

In connection with the recent views on the system of the Lepidoptera the *Cossidae* have often attracted attention.

LINTNER (1885) (nympha).

DYAR (1894 and 1894 *b*).

PACKARD (1895).

QUAIL (1904 *a. b*).

TSOU (1914).

FRACKER (1915).

The remarkable ribbon-shaped, twisted setae have been described and illustrated by LIJONET in 1760 in his famous work on the anatomy of *Cossus*.

The most accurate description is that of QUAIL, who also examined a newly hatched caterpillar of *Cossus cossus*. In doing

this, he discovered the existence of trumpet-like setae, which as he believes, can open and shut. He also discusses *Zeuzera pyrina* and *Culassa expressa*.

Tsou found two punctures upon the prothorax of *Cossus*, identical in appearance with the base of a seta.

Boas (1899) examined the thorax of this kind and found a rudimentary thoracic stigma on the intersegmental membrane between the mesothorax and the metathorax, whilst he takes the little spots, generally considered as rudimentary stigmata, for the rudiments of the wings.

*Cossus cossus.*

*Prothorax:* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis*, *s. subdorsalis superior* and *s. subdorsalis inferior* and a special seta as third in this series; in a little group before the stigma there are three setae, probably agreeing with *s. prostigmatis* and two *s. infrastigmules*. Two *s. basales*, two *s. propedales*, and *s. ventralis*.

A prothoracic shield is wanting but a dark-coloured spot occurs in its place.

*Mesothorax.* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis*, *s. poststigmatis*, a little higher than usual; *s. prostigmatis* or *s. infrastigmatis*, *s. basalis*, *s. propedalis*, *s. postpedalis* and *s. ventralis*.

I draw attention to the fact that in Quails figure of the first instar four setae are marked above the rudimentary stigma (?), and moreover one before, one behind, and two below it, making eight in all, which consequently entirely agrees with my statement, because *s. ventralis* has not been mentioned by him. Tsou distinguishes many more.

*Metathorax* = *mesothorax*.

*Abdomen 1.* *S. dorsalis* (smaller than the others) *s. subdorsalis*, *s. suprastigmatis*, *s. poststigmatis* (higher than usual) and one *s. prostigmatis* which can only be seen with a higher power; two *s. infrastigmatales*, *s. basalis*, three *s. propedales*, *s. ventralis*.  
*Segm. 2* = 1.

On none of my specimens could I find  $A_1$  of Tsou.

*Segm.* 3, 4, 5, 6 = 1, but instead of the three *s. pedales*, there are three *s. propedales*, of which two are placed a little nearer to the caudal part than the third. On the leg no setae are found.

" 7, 8 = 1.

" 9, *S. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. poststigmatis* more ventral than on the other segments, two *s. infrastigmatis*, one of which is so much more ventral than on the other segments, that it comes to lie almost exactly under the other; *s. basalis*, *s. (pro)pedalis* and *s. ventralis*.

" 10. Above the anal opening: *s. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*; under it: lateral three setae = *s. poststigmatis* and two *s. infrastigmatis*; ventral but above the anal legs two setae = *s. basalis*, and *s. propedalis*; and ventral under the anal legs: *s. ventralis*.

*Nympha.* Except the vertical rows of little hooks on the dorsum there are no setae on the nympha.

#### *Zeuzera pyrina* L.

Coll. Kall. Pl. I fig. 26 and 27. Full-grown specimen, length 55 m.m. The last segments have been a little damaged in stuffing.

*Prothorax.* Large paired prothoracic shield. On this I see only two setae = *s. subdorsales*. There may have been more, which have been broken off during the mounting. *S. suprastigmatis* is very small and at the base of it there is no pigment, *s. prostigmatis* is very large, possessing much pigment at its base; right over the stigma a little pigmental spot without seta, *s. propedalis*, *s. basalis*, *s. postpedalis*, *s. ventralis*.

*Mesothorax.* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis* is doubled, *s. prostigmatis* in front of a dark pigmental spot, which was plainly visible when the empty skin was examined, *s. infrastigmatis*, *s. propedalis*, two *s. basales*, *s. postpedalis*, *s. ventralis*. Moreover on the left side, oral of *s. prostigmatis* a seta is found, the base of which is surrounded by much pigment and on the right side a seta caudal of the *s. dorsolateralis* without a pigmental

spot. On the intersegmental membrane between the mesothorax and the metathorax there is a little pigmental spot without a seta. At first I looked upon the spot behind *s. prostigmalis* as a rudimentary stigma and supposed the last-mentioned little spot to be accidental. After having read BOAS, it seems to me a more probable solution that the large spots agree with the wing-rudiment (Pt.) and that the little spot is the rudimentary stigma (St.).

*Metathorax* = *mesothorax*, but one *s. basalis* is absent.

*Abdomen* 1, 2, 7, 8. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmalis*, *s. infrastigmalis* all with a large pigmental spot at the base, a small *s. prostigmalis* which is oral and dorsal of the stigma, *s. poststigmalis* is absent; *s. basalis*, *s. pedalis*, *s. ventralis*.

*Segm.* 3, 4, 5, 6 = 1 but on the leg are three *s. propedales* implanted on the oral side.

„ 9, 10 not clearly visible.

I draw attention to the fact that the imago of *Zeuzera pyrina* L. shows an extraordinarily primitive pattern.

The agreement between *Cossus cossus* L. and *Zeuzera pyrina* L. is exceedingly great, only the prothorax being different. *Cossus* also has two *s. infrastigmales* and *Zeuzera* has only one. I think we may speak of a definite fundamental plan, but are obliged to consider the full-grown specimens at least, as somewhat modified. *S. poststigmalis* occurs in *Cossus* but not in *Zeuzera*, so that *Cossus* has evidently got more setae than there should be according to the fundamental plan and therefore is more modified.

QUAIL (1904) gives two *s. infrastigmales* on *Zeuzera eucalypti*, instar I, but does not indicate a *s. poststigmalis*. Neither does he draw *s. prostigmalis*.

Family *Psychidae*. DYAR (1899), FRACKER (1915). „The setae are very minute in later stages, in many cases it is impossible to find them without a prolonged search. Abdomen with  $\alpha$ ,  $\beta$ ,  $\delta$ ,  $\rho$  (*s. dorsalis*, *s. dorsolateralis*, *s. suprastigmalis*?) in an almost straight line above the spiracle” (Pl. I, fig. 6 after DYAR l. c. p. 179).

Family *Elachistidae*. FRACKER (1915) does not mention the setal pattern.

Family *Coleophoridae*. FRACKER (1915, p. 80): „setae almost indistinguishable, apparently in the normal micro-lepidopteran arrangement”.

Family *Ethmiidae*. The two larvae, examined by FRACKER l. c. p. 81, differed as to the abdomen, the thorax was the same.

Family *Stenomidae*. FRACKER l. c. p. 81, says that  $\rho$  and  $\varepsilon$  are situated below  $\gamma$ , evidently s. dorsolateralis, s. suprastigmalis and s. prostigmalis. Segment 9 is slightly different from the others.

Family *Hemerophilidae*. According to FRACKER (1915, p. 82) this family differs a good deal from the *Yponomeutidae* with which formerly it was sometimes connected. On the prothorax  $\alpha$  (s. dorsalis) is more lateral than  $\beta$  (s. subdorsalis), on the abdomen it is the other way about, except on segment 9, which again resembles the prothorax. The four genera examined differ slightly from each other.

Family *Gelechiidae*. FRACKER (1915), mentions as a distinction from the *Pyrilidae*, the three setae of the K-group; and the distance of seta  $\beta$  on segment 9 as a distinction from the *Tortricidae*. He goes on to say that the genera differ and that the species of *Gelechia* vary greatly (l. c. p. 84).

Family *Oecophoridae*. FRACKER (1915, p. 85) cannot find a satisfactory characteristic to distinguish them from the *Gelechiidae*.

Family *Blastobasidae*. This family differs from all the others in  $\rho$  (= s. suprastigmalis?) on the abdominal segment 8 being caudodorsad of the spiracle and  $\alpha$  cephaloventrad; therefore a s. prostigmalis must apparently be present. FRACKER (1915, p. 86).

Family *Cosmopterygidae*. FRACKER gives on p. 86:  $\beta$ ,  $\delta$ ,  $\rho$  in a transverse line, apparently the same arrangement, which O. HOFMANN (1898) found in some *Pterophoridae*.

Starting from the *Tischeriidae* FRACKER takes the families together as the TINEOID SERIES of the NON-ACULEATA. If we try to find out the constant characteristics, we only can say that the tubercula are monosetal and that there are no secondary setae.

The usual type of the MICRO's is to be found everywhere, but in all groups modifications in place as well as in number of setae occur.

From this point of the series FRACKER passes on to the *Pyralidoidea*, which HANDLIRSCH places before the *Thyrididae* and after the *Geometridae*.

HANDLIRSCH on the contrary goes on to the *Zygaenidae*, and I therefore prefer to insert the ZYGENOID SERIES of the NON-ACULEATA in this place, with the observation that HANDLIRSCH discusses the family of the *Megalopygidae*, belonging to it, a little earlier.

Family *Chalcosidae* and

Family *Dalceridae* were not examined by FRACKER (1915).

Family *Pyromorphidae*. FRACKER (1915, p. 95) finds that these larvae form the transition from a typical Micro into a Slug-caterpillar. These larvae possess verrucae to wit: *v. dorsalis* grown together with *v. subdorsalis*. According to FRACKER's fig. 59 beside these large verrucae occur: *v. suprastigmalis*, *v. infrastigmalis*, *v. basalis*, *v. pedalis*.

The pattern reminds us a little of the *Saturnidae* or the *Lymantridae*.

In the various genera there is some difference in the arrangement.

Family *Epipyridae*. FRACKER says on p. 96 that there is no sign of verrucae and that secondary setae are sparsely scattered over the entire body. In this respect the family differs very much from the former.

Family *Megalopygidae*. FRACKER (1915) considers this family as the transition from the *Zygaenidae* to the *Cochlidiidae*.

There are *verrucae*, on the abdomen: *v. dorsalis* united with *v. subdorsalis*, *v. poststigmalis* consolidated with *v. infrastigmalis*, *v. basalis* and besides on abdomen 1 also one *v. propedalis* and *v. postpedalis*. The thorax is a little different.

Family *Cochlidiidae*. DYAR (1899) has given a synopsis of the *Slug-caterpillars*.

FRACKER (1915, p. 97) only says that the verrucae sometimes have the form of scoli and that some of the genera are entirely smooth.

If we try to find whether this ZYGENOID SERIES possesses a definite characteristic, we see that except the *Epipyridae*, which live as parasites (FRACKER 1915, p. 96), the families are characterized by verrucae which sometimes grow out to scoli and which sometimes disappear entirely. These verrucae are mostly grown together, so that a pattern arises strongly resembling that, which I have called type Ia. From this it differs in some respects, so that no direct descent of the *Saturnidae* from these *Zygaenoidae* can be assumed, but only a parallel development of the pattern.

Family *Zygaenidae*. FRACKER (1915) no statement. In KALLENBACH's collection there are many species represented by larvae which, however, are all fullgrown.

The striking spots do not take origin from the *verrucae*. On the abdomen are: *v. dorsalis* (grown together with *v. subdorsalis*?) *v. suprastigmatis*, *v. infrastigmatis* (united with *v. poststigmatis*?) *v. basalis*. The pigmental spots which occur oftenest are: 1st a spot mediad of *v. dorsalis*, 2nd one in front of it, 3rd one behind it, 4th one behind the stigma, 5th one between *v. infrastigmatis* and *v. basalis*. These spots may be doubled, they may also grow together so that they develop into stripes.

The examination of these caterpillars in the youngest instars might prove important. They are closely connected with the Microlepidoptera, viz. with the ZYGENOID SERIES of the NON-ACULEATA.

#### *Bombycinae.*

This gigantic group of caterpillars has been studied in detail by PACKARD, (1895, 1905, 1915). It is very much to be regretted that through his death the third part of his work has not been completed; the writer would probably have added a general synopsis. All we have now is the very interesting introduction which precedes volume I and which was written without the experience obtained during his study of the enormous material. His work is the only monograph on caterpillars known to me in which all or many instars of nearly all kinds of caterpillars have been described and figured. The magnified setal pattern mostly has

been drawn next to them as a separate figure. I think that we owe this for a great part to DYAR.

PACKARD's classification is most easily studied from his: "genealogical tree of Lepidoptera" (1895, p. 83). He thinks all the *Bombycinae* descend from the *Lithosiidae*, and these from the *Tineina*. The *Sphingidae* descend like the *Saturniidae* from the *Ceratocampidae*. This classification so far concurs with that of HANDLIRSCH (1908). This writer also places the families mentioned in close contact, but thinks they have developed from different ancestors. Against PACKARD's opinion may be adduced, that the *Bombycidae*—*Saturniidae*, the *Sphingidae*, the *Lithosiidae* have all been found for the first time in the beginning of the Caenozoicum, just as the *Noctuidae*, the *Geometridae*, the *Hesperidae* and the *Papilionidae* s. l., which according to PACKARD have all descended with more or less intermediate groups from the *Lithosiidae* and which for the greater part form the extreme branches of his genealogical tree. In 1905 (p. 46) PACKARD gives another classification which is slightly different but yet in principle the same. He thinks the *Notodontidae* descend from the *Thyatiridae*, which HANDLIRSCH places next to the *Hesperidae*. This clashes with the palaeontological data, the *Notodontidae* are the youngest family and are only known from the Quartair.

The series of PACKARD's families is: (according to 1905, p. 46) *Notodontidae*, *Ceratocampidae*, *Saturniidae*, *Hemileucidae*, *Sphingidae* and *Cerucinae* as *Syssphingina*, opposed to which are the *Symbombycina* with *Dataninae*, *Apatelodinae*, *Eupterotidae*, *Ichthyurinae*, *Liparidae*, *Lasiocampidae*, *Endromidae*, *Bombycidae* and *Brahmaeidae*.

I have arranged the families according to PACKARD and wish to point out HANDLIRSCH's series: *Bombycidae*—*Saturniidae*, *Lasiocampidae*, *Sphingidae*, *Liparidae*, *Notodontidae*. At the end of this discussion I shall return to this subject.

Family I. *Notodontidae*. This large family contains seven subfamilies, of which according to PACKARD (1895) some (the first four) are

to be considered as the original forms of the *Symbombycinae*, others (the last three) on the other hand belong to the *Syssphingina*. The general pattern of setae is according to type I, in one sub-family there are verrucae even in instar I, in others they appear later on.

1. Sub-family *Gluphisinae* is difficult to separate from some of the *Notodontinae*. Some larvae are smooth, *Gluphisia septentrionalis* possesses glandular hairs (PACKARD 1895, Pl. VIII, p. 91) which are very shortly forked and afterwards disappear.

According to fig. 1b, the pattern on the abdomen is: *s. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis*, *s. subdorsalis sup.* and *inf.* *s. prostigmatis*, *s. infrastigmatis* which is placed very orally, six *s. basales*, in instar I, whilst in instar II *s. dorsolateralis* and *s. subdorsalis inferior* disappear. The presence of these two setae in instar I is very important.

2. Sub-family *Apatelodinae*. The young larvae are covered with long white setae, which are standing on verrucae according to Type I, with *v. subdorsalis inferior* (PACKARD 1895, Pl. IX).

3. Sub-family *Pygaerinae*. PACKARD (1895) makes a distinction between the colour of the primary and secondary setae in the full-grown larvae. PACKARD (p. 105) thinks that this sub-family is the most generalized one of the family. As far as I can see on Pl. X—XIV the pattern of the *Datana* species agrees with *Phalera bucephala*. In connection with the origin of the stripes, which I was able to observe in a Pygaerine, this is of much importance, just as the presence of an 11<sup>th</sup> abdominal segment.

To outline the family in an easier way, I have put the description of *Phalera bucephala* L. after the discussions of the sub-families p. 65 sqq. (On the origin of the stripes see chapter VII and VIII).

FRACKER (1915) does not discuss the setal pattern.

4. Sub-family *Ichthyurinae*. *Ichthyura apicalis* (PACKARD 1895, Pl. XV) has setae, *I. inclusa* and *I. albosigma* (l. c. Pl. XVI) verrucae according to type I.

5. Sub-family *Notodontinae*. According to PACKARD (1895, Pl. XVII—XXIII) the larvae possess setae according to type I.

6. Sub-family *Heterocampinae*. Larvae sometimes with stema-

topoda (*Macrurocampa*). Larvae (PACKARD 1895, Pl. XXIV—XXXV) with setae according to type I, sometimes with a small *s. prostigmalis*: (*Hyarpax aurora*, *Schizura unicornis*).

It is remarkable that PACKARD in 1905 (p. 44), while discussing the setal pattern does not figure the *s. prostigmalis* on *Schizura*.

Exceedingly peculiar setae resembling antlers are born by *Heterocampa* during instar I, later on they disappear. They seem to agree with *s. dorsalis* of the prothorax (l. c. Pl. XXX).

7. Sub-family *Cerurinae*. Long stematopoda, setae according to type I (PACKARD 1895, Pl. XXXIV—XXXVII).

### Sub-family 3. *Pygaerinae*.

*Phalera bucephala* Linn. Plate III, fig. 7—13.

Material in alcohol. Collected at Groningen, summer 1915.

In this caterpillar the head becomes coloured last, while in nearly all others the head is black immediately after moulting and the tubercles become coloured afterwards.

Instar I. Duration 9 days. Length  $2\frac{1}{2}$  mm. The tubercula are not black. The setae are not plumed.

*Prothorax*. *V. dorsalis* in front of the prothoracic shield, consisting of three setae, about  $\frac{2}{3}$  mm. long, they are not united.

*V. subdorsalis*. Three setae which are longer than 1 mm., implanted on a tuberculum, which is clearly higher than the prothoracic shield. *V. suprastigmalis* has also three setae of a length of not quite  $\frac{1}{2}$  mm., concentrated on a tuberculum which in most individuals has coalesced with the prothoracic shield.

No *s. dorsolateralis*, *v. poststigmalis* with some (mostly 3 or 4) setae, if at least they have not become combined with the prothoracic shield, *seta infrastigmalis*, *v. basalis* with two setae. No *s. pedalis* and no *s. ventralis*.

*Mesothorax* and *metathorax*. *V. dorsalis* with three setae, *v. dorso-lateralis*, *v. suprastigmalis* and *v. infrastigmalis*, each of them with two setae. *V. basalis* is not distinctly outlined, there are two setae which are not joined together.

No *s. pedalis* or *s. ventralis*.

Abdomen 1, 2. *V. dorsalis* with two setae, so that I presume *s. dorsolateralis* has been added to them, *s. subdorsalis*, *s. suprastigmatis*, *s. infrastigmatis* and *s. poststigmatis* each of them with one seta. *V. basalis* with two or three setae and on the place where there is a leg in the segments 3—6 one seta = *s. pedalis*. Segm. 3, 4, 5, 6 = 1, but one *s. basalis* is missing, whilst there are along the outer and the lower edge of the leg mostly five or six rather long setae ( $\pm \frac{1}{2}$  mm.) I consider these to be the *s. pedales*. It may be possible, however, that the *s. basales* of 1 agree with these *s. pedales* of segm. 3—6 and that the seta there called *s. pedalis* really is a *s. ventralis*. This supposition appears especially probable, when the caterpillar is looked at from the ventral side and, starting from segment 3, we try to explain the arrangement of 4. If, on the other hand, the caterpillar is looked at from the lateral side and segment 1 is started from, we hesitate to give the above explanation for segment 3.

„ 7, 8, 9 = 1.

„ 10 = 1. *S. dorsalis*, close to it lies *s. suprastigmatis*. These is a *s. basalis* and the setae forming together the *s. pedales* are very strong and are  $\pm \frac{3}{4}$  mm. long.

„ 11. Behind the setae of 10 there are on the anal flap three more setae which are arranged in the following way:

*s. dorsalis*. *s. subdorsalis*, *s. suprastigmatis*.

Instar II. Duration 10 days. Length 7 mm. The arrangement of the setae is almost the same as during instar I. The setae are not plumed either, but the tubercula are black and on the front and the back edge of nearly all the segments there is a black spot bearing many setae, which are smaller than those on the primary tubercula. In the figure I have marked the median spots with a darker colour than the paired ones. The tubercula of the other side, which are visible on Pl. III, fig. 10, lateral aspect, are striped.

*Prothorax.* The prothoracic shield has disappeared.

*V. dorsalis* very large and protruding, provided with 3—8 setae, more than 1 mm. long. *V. subdorsalis* small, consisting of some setae behind the large *v. dorsalis*. *V. suprastigmatis* with three setae just as *v. prostigmatis*. Of this last wart the setae are smaller. Under the stigma one seta = *s. infrastigmatis*. *V. basalis* with three setae. On the leg some smaller setae.

*Mesothorax.* *V. dorsalis*, *v. dorsolateralis*, *v. suprastigmatis*, all of them with two setae. *Seta prostigmatis* and *seta basalis* with one seta. At the back edge of the segment a black dorsal spot with very short setae.

*Metathorax* = *mesothorax* but *v. prostigmatis* has two setae and *v. basalis* four. Further there are two small setae behind *v. prostigmatis* and just over the leg on the front side is *v. pedalis*.

*Abdomen* 1, 2. Two median shields occur at the oral and caudal edge, of which especially the latter bears many small setae.

*V. dorsalis* with two setae, *seta subdorsalis*, *s. suprastigmatis*, *s. poststigmatis* and *s. infrastigmatis*, all of them  $\pm \frac{1}{2}$  mm. long. One row mostly of five *s. basales*, and one large *s. pedalis*.

*Segm.* 3, 4, 5, 6 = 1, but the large *s. pedales* of instar *I* are absent here, and instead there are 4—6 large setae above the leg = *s. basales*. On the leg itself there is a large spot with small setae = *s. pedales*. One gets the impression that the *s. pedales* of instar *I* are placed higher. Beneath *s. subdorsalis* a spot or a seta.

" 7, 8 = 1.

" 9 = 1 but *v. suprastigmatis* has two setae. *S. poststigmatis* is absent. No median dorsal shields are found.

" 10. All the setae situated above the stigma from the left to the right side are placed on an anal shield. These setae are  $\pm 1$  mm. long. Further there are on this segment no setae, except a few on the outside and inside of the leg, which are  $\pm \frac{3}{4}$  mm. long.

Instar *III*. Length  $\pm 15$  mm. The number of spots with small

setae between the primary warts and setae has increased. Moreover there occur some scattered setae. The setae on the primary tubercula are  $\pm 1-1\frac{1}{2}$  mm. long. The longest which are at the same time the biggest, are found on the prothoracic shield and on the anal shield.

*Prothorax.* On the prothoracic shield three setae, which in my opinion represent *s. dorsalis*, *s. dorsolateralis* and behind it a small one = *s. subdorsalis*. *V. suprastigmatis* has three setae just as *v. prostigmatis*. The seta behind *v. suprastigmatis* is also plumed. *V. basalis* with three setae. The small setae on the leg are not feathered.

*Mesothorax* and *metathorax.* On the front-edge of the segment a double row of spots, on the hind edge one row.

*V. dorsalis* has three setae, *v. dorsolateralis* just as *v. suprastigmatis* has two. There is a single seta *prostigmatis*. One large *v. basalis* and many small setae which, however, are not fixed on black tubercula.

*Abdomen* 1—10 as in instar *I*, but:

*Seta infrastigmatis* is single. Three setae, which are not united and not implanted on a tuberculum, stand instead of *v. poststigmatis*. The number of *s. basales* amounts to  $\pm 10$ .

Instar *IV.* Length  $\pm 25$  mm.

Apparently this instar completely resembles the full-grown form. Small setae, not plumed, are to be found everywhere. The spots have become more numerous and bear setae of  $\pm 1$  mm. long. Still more than in instar *III* they are arranged in horizontal and vertical rows and thereby give the impression of forming stripes.

The primary tubercula may be recognised by the seta which are longer (mostly  $1\frac{1}{2}$  mm.), and generally thicker too. They have short plumes. On each wart there are more setae than before, which is rather striking as during instar *I*, *II* and *III* the number is almost constant.

As examples of the most intricate pattern of spots I chose the prothorax and abd. 5, the others agree with these *mutatis mutandis*.

*Prothorax.* There is a large prothoracic shield which on each side has two very long setae (3 mm.) and behind them two or three shorter ones ( $\frac{3}{4}$  mm.). These taken together I consider to be *v. dorsalis* and apart from them is one seta corresponding with *s. subdorsalis*. *V. suprastigmalis* and *v. dorsolateralis* over the clearly visible *v. prostigmalis*. *V. prostigmalis* projects a good deal and has three setae, *v. basalis* four. Over the stigma are two tubercula with five and two setae. They take their origin from the spots which have appeared in instar *III*.

*Abdomen 5.* Both the median dorsal shields, arisen during instar *II*, are still present. The *verrucae dorsales*, *v. subdorsalis*, *v. suprastigmalis*, *v. poststigmalis* are clearly visible. The permanency of this last wart is interesting as it showed an inclination to dissolution in instar *III*. *V. infrastigmalis* consists of some scattered setae. There are less *setae basales* than in instar *III*, there is also a *v. pedalis* present in the form of a spot. Other spots are: on the front edge under the median shields a large one and two smaller ones of which the 2<sup>nd</sup> lies in front of *v. suprastigmalis*, next come a large and a small one about on the same height as the stigma and *v. poststigmalis*. Behind the first smaller spot of this row we find two a little larger, and behind these in the same row *v. subdorsalis*. Over *v. poststigmalis* is a very large spot, which lies therefore in one row with the 2<sup>nd</sup> large spot of the 1st vertical row. Under *v. poststigmalis* are small spots with long setae which I first took to be primary ones because of their length. They lie in a row with *v. infrastigmalis*. Over the *setae basales* is a long-drawn spot. In different individuals and in different segments of one individual, these spots and tubercula vary a little in form and size. Most of them resemble the above example and one can always recognize the same primary tubercula.

Instar *V*. Length 40 m.m.

The primary tubercles can not be found. All the setae are somewhat plumed and are  $\pm 2$  m.m. long. The spots have almost grown together to stripes. Round each seta is a little area free from pigment. Over the stigma are, the dorsal median included,

three stripes agreeing with the row of spots running through *v. subdorsalis*, *v. suprastigmatis* and the spots over the stigma. There is no clear stigmatic stripe. The infrastigmatic stripe is distinct on the front and back edges of the segment, the basal stripe is narrow, and there is a clear, broad pedal stripe.

*Pupa.* I could not find any sign of a pattern.

Family *Eupterotidae*. FRACKER (1915) includes *Apatoleles* which deviates in respect to the tubercula. I think that he is right as regards the larva.

Family *Liparidae* = *Lymantridae*. The tussock-moths can be divided into two groups, those with and those without pencil-shaped setae. Several of them have long since drawn the attention of investigators because of their peculiar pattern, the thick tussocks of setae and because of the sexual dimorphism of the caterpillars.

#### Literature:

SWAMMERDAM (1737), *Orygia* ♀ and ♂ caterpillar, pupa with setae.

HÜBNER (1766), development of the setae.

RILEY (1885), *Orygia*.

WACHTL AND KORNAUTH (1893), particular setae of *Oeneria*.

PACKARD (1889 and 1893), development of *Orygia*.

FRACKER (1915), synopsis of the family.

The last mentioned writer says (l. c. p. 104 sqq.) that *Porthetria*, *Gynaephora* and *Euproctis* have the ordinary verrucae like the *Arctiidae*, except that there are three verrucae on the mesothorax and the metathorax above the K-group.

He thinks that the coalescence of  $\alpha$  with  $\beta$  which occurs in *Porthetria* = *Lymantria* (therefore of *v. poststigmatis* with *v. suprastigmatis*) is unique. He examined *Euproctis* = *Porthesia* but did not observe the same arrangement there. The second group has pencils, to this belong *Olene*, *Hemerocampa* and *Notolophus* = *Orygia*.

FRACKER does not attach much importance to the question whether  $\alpha$  and  $\beta$  (i. e. verruca dorsalis and subdorsalis) coalesce or not.

I examined three complete series, my principal results are:

1. The coalescence of *v. suprastigmalis* with *v. poststigmalis*.
2. The disappearance of *v. dorsalis* in different ways.
3. The structure of the setae becoming more intricate in the course of the successive moultings.
4. The presence of peculiar setae on *Lymantria dispar*.
5. The disappearance of the prothoracic shield.
6. The presence of verrucae on the pupa, to which SWAMMERDAM (1737) already drew attention.
7. The verrucae on the larva are arranged according to type **I** or to type **Ib**.

Family *Liparidae* Linn. Plate II, fig. 8—11.

*Lymantria (Onceria) dispar* L.

Material in alcohol and living animals (summer 1915). In the successive instars of caterpillars the same pattern is always found, the tubercles are warts with many setae.

Instar *I*. Duration 12 days. Length 4 mm. The setae are different in form viz.:

1. Very short feathered, light coloured ones, with a length of  $\pm 1\frac{1}{2}$ —2 mm. (the side-branches are  $\pm 7 \mu$ ). The base is enclosed in the black case of the wart.

2. Not feathered ones, mostly 400—500  $\mu$ . long and coloured deep brown (Pl. II, fig. 10). The lower part is  $\pm 100 \mu$  long and a little narrower than the elevation of the wart on which the seta stands. A little bladder follows, with almost colourless wall. The diameter is  $\pm 20 \mu$ . Through the presence of this bladder movements of the top part of the seta are rendered possible. This part is  $\pm 300 \mu$  long and tapers into a point. At first I thought that these peculiar setae were of use during hatching, as I imagined that before and during the removal of the skin, they were folded up. The examination of newly hatched larvae showed me, however, that there these setae already stand upright. The number of the bends is decidedly not larger than afterwards. I surmise that the same organs occur in the closely related *Lymantria monacha*. According to SHARP (II, p. 407), WACHTL AND KORNAUTH (1893)

think that there they serve for the dispersion of the larvae by the wind. In that case, however, they should have been much longer, for these small vesicles with a radius of  $\pm 10 \mu$ , cannot exercise any influence on the specific weight. Moreover, the long setae are more suitable for this purpose. It is certainly remarkable that these setae only occur in the first instar both on *Lymantria dispar* and on *Lymantria monacha*. Their function is a riddle to me; for the time being, I identify these setae with the glandular hairs which often occur in a first instar. Directly after hatching, the head is coloured black, the tubercula become coloured later on.

The following tubercula are visible:

*Prothorax*. Small *v. dorsalis* with short setae, rather large *v. subdorsalis* on which the setae mentioned sub. 2 are present (this verruca is connected with the preceding one by an indistinct prothoracic shield); a far projecting *v. suprastigmatis* with which *v. prostigmatis* is connected, *v. infrastigmatis*, *v. basalis* and one *v. ventralis*.

*Mesothorax* and *metathorax*. Very large *v. dorsalis*, small *v. dorsolateralis*, large *v. suprastigmatis*, a long drawn *v. infrastigmatis*, *v. propedalis*, *v. basalis*, *v. ventralis*.

*Abdomen* 1. Very small *v. dorsalis* and an extraordinarily large *v. subdorsalis*. The verruca over the stigma is divided into two parts by a furrow. The front part is *v. suprastigmatis*, the back part *v. poststigmatis*; *v. infrastigmatis* is elongated, *v. basalis* small, no *v. pedalis*.

This pattern I have called type **I b**.

*Segm.* 2 = 1, but *v. infrastigmatis* consists of two parts, one behind the other.

" 3, 4, 5, 6 = 2, but *v. basalis* is absent.

" 7, 8, 9 = 2, but on 9 the verrucae are much higher than on the other segments.

" 10 is strongly reduced, the verrucae are not distinct.

*Instar II*. Duration 12 days. Length 8 mm. The same as instar *I*, but the peculiar setae have disappeared. The setae bear

somewhat longer plumes, *v. dorsalis* becomes smaller. The prothoracic shield has disappeared.

Instar III. Duration 8 days. Length 15 mm. As instar II.

Instar IV. Duration 6 days. Length 24 mm. As instar II, the sides of the head become grey.

Instar V. Duration 11 days. Length 35 mm. As instar II but some secondary setae appear on the body and the *v. infrastigmatis* are sometimes divided into many pieces, on the thoracic segments the *v. pedales* are wanting.

#### *Pupa.*

On the abdomen of the pupa the verrucae are arranged in a distinct way according to type I b. The furrow between *v. suprastigmatis* and *v. poststigmatis* has grown larger.

The setae on the pupa too are plumed. Distinct are: *v. dorsalis* even larger than on the caterpillars, *v. subdorsalis*, *v. suprastigmatis* + *v. poststigmatis*, *v. infrastigmatis*, *v. basalis* and a far projecting *v. pedalis*.

*Euproctis (Porthesia) chrysothoe* Linn., Plate II, fig. 12—15.

Material in alcohol, from Groningen (spring 1915) and living material from the Hague (autumn 1914).

I have not been able to obtain the newly hatched caterpillars of this species. The youngest are of December 19<sup>th</sup> 1914. They were found in a nest on *Hippophaes rhamnoides* Linn. and as in the course of their development they cast the skin four times, and were only 4 à 5 mm. long, I have described them as instar I.

Instar I. Duration at least 130 days, they hibernate. The first moulting took place on April 27<sup>th</sup>. Length 4 mm. Tubercula formed like warts.

The setae are not plumed,  $\pm 1$  mm. long.

The colour pattern is very intricate, there is a distinct median dorsal line.

*Prothorax.* Both the *v. dorsales* from the left to the right are connected by a distinct prothoracic shield. The *v. subdorsales* are

also connected by a shield which is smaller, however, than the former.

The *v. suprastigmalis* projects very much.

Small *v. infrastigmalis*, very large *v. basalis*. No *v. pedalis*.

*Mesothorax* and *Metathorax*. *V. dorsalis*, *v. dorsolateralis* and *v. suprastigmalis* all equally large. No *v. infrastigmalis*. Very large *v. basalis*. On the median side, close to the leg a small *v. pedalis*.

*Abdomen* 1, 2. *V. dorsalis* large, united with that of the other side. They have a dense bundle of coloured setae, length  $\pm \frac{1}{2}$  mm.

*V. subdorsalis* smaller than on the other segments. *V. suprastigmalis*, and *v. infrastigmalis* are very large, *v. basalis* small and *v. pedalis* also.

*Segm.* 3, 4, 5, 6. *V. dorsalis* is wanting in most individuals. Very large *v. subdorsalis*, large *v. suprastigmalis* and *v. infrastigmalis*. Elongated but very slender *v. basalis*, and on the front edge of the leg a small *v. propedalis*, on the leg some setae.

„ 4 and 5. *V. dorsalis* is present and is even rather large.

„ 6. *V. dorsalis* is small and between the *v. subdorsales* is a median brown elevation.

„ 7 = 6. *V. pedalis*, however, is placed more backwards, about on the spot where the legs are joined to the segments 3—6.

„ 8 = 7, without the median elevation. *V. basalis* is closer to *v. pedalis*.

„ 9. *V. dorsalis* is absent and *v. infrastigmalis* is small; the *v. subdorsales* of the left and right sides are united into one shield. For the rest as 8.

„ 10. Small but strongly projecting *v. subdorsalis*, *v. suprastigmalis*, *v. infrastigmalis*. No *v. basalis* and very small *v. pedalis*.

Instar *II* = *I* but the prothoracic shield has disappeared and the setae are distinctly feathered except the scattered ones on the legs. The *v. dorsales* of the segments 6 and 7 have disappeared. *V. suprastigmalis* is divided into two parts as in *Lymantria dispar*. This I consider to be a coalescence of *v. suprastigmalis* and *v. poststigmalis* and I think I could also observe this in Instar *I*.

Instar *III*, *IV*, *V* = instar *II*.

During instar *V* a dark spot is generally present on the meso-

and metathorax, on the place where the stigma should have occurred, if it had been placed on the back edge of the segment, as is the case on the prothorax. At first I considered this spot to be a rudimentary stigma, but after having read BOAS (1899) and after a repeated examination, I take it to be a transparent wing-rudiment.

The appearance of this spot in Instar *V* proofs the latter suggestion to be the right one.

*Orgyia antiqua* Linn.

Most writers only mention the beautiful colours, the pencils and the tussocks of this larva, these attributes being generally found in the members of this family.

The principal statements are:

BUCKLER (III, p. 11 and 12) gives an excellent description of the fullgrown caterpillar, but of course without mentioning the position of the tubercula. Of the first stages, however, he says very little. Thus for instar *I* he only mentions that the tubercula are black, and that after the fourth moulting (instar *V*) they are red. The tussocks on the segments 5 and 6 in instar *IV* show a kind of black hue, those on 7 and 8 a sort of white. After the 4th moulting they are all white, later on, during this stage, they become brown. In instar *I* a broken subdorsal line was seen.

His drawings (Pl. XXXIX, fig. 1, 1a, 1b) give different variations of colour. My specimens agree for the greater part with fig. 1. It seems to me that his fig. 1b shows the same mistake as that of HÜBNER.

HOFMANN-SPULER (1910) says that the ♂ caterpillars are smaller and that they have yellow bristles on the back, whilst the large ♀ caterpillars are provided with yellow-brown bristles. In this he agrees with SWAMMERDAM (1737). His drawings (Pl. 15, fig. 25a b) are very bad.

JACOB HÜBNER gives as a frontispiece to his book in four volumes on caterpillars, a drawing of *Orgyia antiqua*, of which the length of the body without the setae is 11 cm. and with the setae 21 cm.

The drawing is certainly large enough to justify the expect-

tation of a great accuracy in the arrangement of the tubercula. On examining it closely, however, one sees that on each segment a verruca is left out. *V. suprastigmalis* was drawn excessively large and thereby the *v. infrastigmatales* were placed too low, so that no room was left for a *v. basalis*, though the legs are plainly visible from the side and it should therefore have been represented. On the prothorax *v. subdorsalis* has not been drawn, though in reality it is present, and the false impression is given that *v. dorsalis* is as much developed as *v. suprastigmalis*. In fact the latter projects a considerable distance from the body and the former is visible as a median protuberance on the base of it.

I have treated this case somewhat in detail, because it shows that the confidence, which I originally placed in existing illustrations, was misplaced.

DYAR (1894) defines the *Lymantridae* with the following words:

"Not more than one tuberculum on the third annulet and only six above the base of the leg.

"Not more than two tubercula on the middle annulet, and generally one on the third; one prothoracal shield.

"Tubercula IV and V (*v. poststigmatis* and *v. infrastigmatis*) far from each other or IV has disappeared. Tubercula with many setae, no setae on the skin."

PACKARD (1889, p. 55—59) gives the fullest description.

As has already been observed, he describes only four stages, whilst BUCKLER gives five; my investigation has also shown me that there are five different instars.

PACKARD gives as the most important results:

Instar *I*. Duration 7—8 days. Length 4 mm., tubercula black, the middle ones on the thoracal segments smaller than the lateral ones. Setae thinly spinose, very long. The two glands on the abdominal segments 6 and 7 not clear.

Instar *II*. Duration 4 days. Length 6—8 mm. Tubercula black; except the two large lateral ones on the 1<sup>st</sup> thoracal segment which are red at the base. The glands are coral-red. There is a subdorsal line which is not quite complete. Towards the end

of this stage there appear some plumed setae on the dorsal tubercula of the 8th (abd.) segment and sometimes on the same tubercula of the 1st and 2nd (abd.) segments.

Instar *III*. Duration 5 days. Length 10 mm. The lateral tubercula of the prothorax are of a pale Indian red, with black in between and form a pencil of plume-like setae which grow thicker towards the end and which are as well developed proportionally as those of the full-fed larva.

The four median dorsal tufts are well developed, the two front ones are deep brown, the two back ones are white. The 8th (abd.) segment also has a long pencil of plume-like setae. All the lateral tubercula are of a bright flesh-coloured red. With some the colour of the dorsal tufts changes.

Instar *IV* (= last). Duration 7—14 days. Length 17—? mm. The ♂ ones sooner develop into pupae than the ♀. The dorsal tufts become pale buff-yellow. The tubercula are of a bright coral-red, except the dorsal ones of the segments 2 and 3 which are of a bright yellow.

The data which PACKARD gives make it appear that this larva only possesses four instars in America. The report of the 2nd moult on May 22nd (p. 55) is probably due to a mistake, apparently the 1st moult is meant, as the hatching took place on May 15th.

*Orgyia antiqua* Linn. Plate III, fig. 1—6.

Material in alcohol from June till August 1915 and of instar *I*, *II* and *III* also of June 1914. Collected at the Hague and Groningen.

Instar *I*. Duration 6 days. Length 3 mm. At the hatching the head is black, the tubercula are light grey, they get coloured half an hour later and become black.

The colour-pattern is very intricate, but the colours are not proof against the influence of alcohol. This is also the case during the following stages, so that I do not mention them here.

See PACKARD (1889, p. 55—59).

The *v. subdorsales* are triangular and the setae which are fixed

on them point in all directions. The other verrucae are mostly elliptical with a long horizontal axis. The setae are arranged more or less in one line, the middle seta is mostly the longest and the others get symmetrically smaller in regard to this one. The longest setae are born by the *v. suprastigmatales*. The setae are not plumed.

*Prothorax*. There is a small *v. dorsalis*, a very large *v. subdorsalis* which is connected with the corresponding verruca of the other side by a black coloured prothoracic shield. By this the small *v. dorsales* get united. Moreover, there is a rather large *v. suprastigmatis* which projects a good deal, a *v. infrastigmatis*, which has an offshoot pointing towards the dorsum, which perhaps corresponds to the missing *v. prostigmatis* and a *v. basalis* just over the beginning of the leg.

*Mesothorax* and *metathorax*. There occur: *v. dorsalis*, *v. dorsolateralis*, a little larger than the *v. dorsalis*, *v. suprastigmatis*, *v. infrastigmatis* and a small *v. basalis*. The setae on these segments are shorter than those on the other. One might be inclined to think that *v. dorsolateralis* owed its origin to the shifting of *v. subdorsalis*. This verruca on the mesothorax and metathorax is placed in front of *v. dorsalis* and on all the abdominal segments *v. subdorsalis* lies behind it. Besides in other families the same arrangement occurs as in this one, but then there is also a verruca or seta in the place where *v. subdorsalis* lies. For these two reasons I think that the name of *v. dorsolateralis* deserves the preference. (See Chapter IV).

*Abdomen* 1, 2, 3, 4. There are a small *v. dorsalis*, a large *v. subdorsalis* which is prolonged in a triangle towards the oral side, beneath the *v. dorsalis* a *v. suprastigmatis* which has the longest setae, a *v. infrastigmatis* and a small *v. basalis*.

*Segm.* 5. *V. dorsalis* is very small in some individuals and totally absent in others, for the rest as on the abdomen 1.

„ 6. *V. dorsalis* is very small and generally bears only one short seta, for the rest = 1.

„ 7 = 1. In some individuals *v. dorsalis* has been partly split into separate setae.

Segm. 8 = 1. Two *s. basales*.

- " 9. No *v. dorsalis*, *v. subdorsalis* and *v. suprastigmatis* very large and strongly projecting, *v. infrastigmatis* about as large as on 8, a wreath of *s. basales*.
- " 10. It is difficult to reduce the verrucae to the pattern of the former segments. I consider the wart under the anal opening as a *v. infrastigmatis*.

It seems to me that the two *setae basales* of segm. 8 are pseudo-primary ones. If the newly-hatched larvae are examined many individuals with a well developed wart are found. Most parts do not become coloured, but only the two extreme setae. I do not think therefore that this case should be taken as a proof of the thesis that warts have taken their origin from simple tubercula, but I think we have to deal with the secondary dissolution of a wart into simple setae.

The two dorsal glands which are so obvious in the following instar on the segments 6 and 7 are faintly visible.

Instar II. Duration 10 days. Length 6 mm.

All the setae are short-plumed, the side branches arise at irregular distances. The form of most warts is about the same as of those of instar I. The setae are not very different in length.

*Prothorax*. *V. dorsalis* is small and is connected with that of the other side by an indistinct prothoracic shield; a very small *v. subdorsalis* which is remarkable in connection with the size it possesses in instar I, neither is it connected anymore with the prothoracic shield. *V. suprastigmatis* is very large and projects considerably. On it are the longest setae (2 mm., short feathered) and between these are mostly five short ones, which are much thicker and have longer plumes. It is an exception when they are longer than  $\frac{3}{4}$  mm. *V. infrastigmatis* is small and is no longer so tall, *v. basalis* too is small.

*Mesothorax* and *Metathorax*. We find the following small warts: *v. dorsalis*, *v. dorsolateralis*, *v. suprastigmatis*, *v. infrastigmatis*, *v. basalis*.

*Abdomen* 1. *V. dorsalis* is small, *v. subdorsalis* very large with

longer setae ( $1\frac{1}{2}$  mm.) than in instar I, *v. suprastigmatis*, *v. infrastigmatis* and *v. basalis* about as in instar I.

*Segm.* 2 = 1, but *v. subdorsalis* is still larger and grows along the ventral edge of *v. dorsalis* in the oral direction.

" 3, 4 = 1, but on the leg we find a black spot with a number of small setae which are only partly plumed. This spot I consider to be a modified *v. pedalis*.

" 5 = 1, but *v. dorsalis* is wanting.

" 6 = 3, but *v. dorsalis* is absent and in the median line a red elevated gland is visible, which has the form of a champagne-cork.

" 7 = 6, but there is no *v. pedalis*.

" 8 = 7. Without the gland. The two *v. subdorsales* of the left and right sides are placed very closely together and also have the particular setae mentioned in segment 1.

" 9, 10 = 7. Moreover, the wart of segment 10 of instar I which was considered to be *v. infrastigmatis* is well developed.

Instar III. Duration 11 days, length 10 mm.

*Prothorax.* There is no longer a prothoracic shield. *V. dorsalis* is small, lying against the median side of the very large, far projecting *v. suprastigmatis*. On the top of the last wart we find short plumed setae of a length of  $\pm 2$  mm. Amidst these are shorter ones ( $\pm 1\frac{1}{2}$  mm.) of which the side branches are a little longer. Towards the end of the setae these side branches grow somewhat longer and thicker and are placed more closely together. Each of these peculiar setae reminds one a little of a French plumeau (feather mop) or of one of the feathers on the head of a *Goura victoriae*. *V. subdorsalis* is small, *v. infrastigmatis* large, *v. basalis* very small.

*Mesothorax* and *Metathorax* as in instar II.

*Abdomen* 1, 2. *V. dorsalis* and *v. subdorsalis* have united with each other and also with those of the other side. This method of origin is still clearly visible. They bear one tuft of setae,  $\pm 1$  mm. long, which show longer and thicker side-branches than the setae generally possess, and they are of a deep brown colour.

*V. suprastigmalis* is large, just as *v. infrastigmalis*. The setae of these tubercula are  $\pm 2\frac{1}{2}$  mm. long. *V. basalis* is small.

Segm. 3, 4. *V. dorsalis* is absent, the *v. subdorsales* of the left and right sides have coalesced. They have setae as those of segment 1, but are a little shorter and are white in colour. For the rest as in instar *II*.

„ 5. *V. dorsalis* is absent, the other tubercula as in instar *II*.

„ 6, 7 as in instar *II*.

„ 8. The two *v. subdorsales* of the left and right sides are united, but not coalesced. They project higher than in instar *II*. The setae closely resemble those of the segments 1 and 2.

„ 9, 10. *V. infrastigmalis* of 10 remains large.

Instar *IV*. Duration 8 days. Length 15 mm.

*Prothorax*. *V. dorsalis* is small and is now to be found as a protuberance placed in the median line on the base of the strongly developed *v. suprastigmalis*. On its top is a black spot on which are implanted short plumed setae,  $\pm 3\frac{1}{2}$  mm. long and two tufts of plumose setae viz.  $\pm 1-1\frac{1}{2}$  mm. and  $\pm 2\frac{1}{2}-3$  mm. long. Each group consists of  $\pm 6-10$  setae. There are no transitions between these two, so that they clearly form two storeys. The longest ones also have the largest side branches. The other tubercula are as in instar *III*.

*Mesothorax* and *Metathorax*. As in instar *III* but *v. dorso-lateralis* has grown smaller.

*Abdomen* 1, 2. The four warts which in instar *III* began to coalesce, now form a whole. For the rest as in instar *III*.

Segm. 3, 4 = 1. It should be observed that here *v. dorsalis* has not been united with the median shield, but has disappeared. The colour and the form of the setae now agree with those of segment 1.

The other warts on this segment and on the following segments correspond with those of instar *III* but:

„ 8. The two *v. subdorsales* are almost united and between the many plumed setae some plumose ones are found as on the prothorax.

Instar *V*. Duration 10—20 days. Length 23—30 mm. For this stage I made an exception where the drawings are concerned. I did not draw the objects themselves under the microscope with the aid of a camera, but took the outline of JACOB HÜBNER'S old frontispice (1766) and in this entered the different tubercula.

The changes are not so great as in instar *IV*.

PACKARD does not describe this stage (see p. 76).

*Prothorax*. The plumose setae have a length of 5 and 10 mm. and stand out above the short feathered setae.

*Mesothorax* and *Metathorax*. As in instar *IV*.

*Abdomen* 1. *V. infrastigmalis* has a tuft of bright yellow setae,  $\pm 7$  mm. long, short plumed, for the rest as in instar *IV*.

*Segm.* 2 = 1. *V. infrastigmalis* is provided with a little group of plumose setae, the length of which is  $\pm 7$  mm.

" 3 to 7 as in instar *IV*.

" 8. The *v. subdorsales* have a tuft of setae of different forms. Between the short plumed setae which are more than 7 mm. long, we find plumose ones of a length of  $\pm 10$  mm. and long feathered ones,  $\pm 5$  mm. long. Further as in instar *IV*.

" 9. The *v. subdorsales* are not united and have each a tuft of very long, short plumed setae and some (2 to 4) plumose ones, the length of which is 5 mm.

The differences between PACKARD'S views and mine follow here in a short synopsis.

PACKARD.

Setae are already spinose in instar *I*.

The feathered setae towards the end of instar *II* on segment 8.

The plumed setae in proportion as large as on the full fed caterpillar in instar *III*. They appear at the same time on the prothorax and segment 8.

Whole duration of all the instars as caterpillar: 23—30 days.

Three moults.

SCHIERBEEK.

In instar *II* spinose or plumed setae for the first time.

Immediately after the moult on prothorax and segment 8 setae which differ from the rest. The plumose ones shorter than the ordinary setae in instar *III* and *IV*. Those of segment 8 only come in instar *IV* and are still very short.

Whole life as caterpillar is 45—55 days. Four moults.

I hope that these differences may give rise to new investigations.

It also seems to me that the histological structure of these setae and the manner of their origin within the more simply organized ones of the former instar, are worth while examining.

I draw attention to the fact, that J. H. KRUMEL in his investigations on the feathers of the Gallinae (1916) also found a more composite structure in the successive "editions of feathers" which appear after the different moults.

Family *Lasiocampidae*. FRACKER (1915, p. 103) thinks there are too many setae to be able to describe them. Some genera are characterised by a dorsal horn on segment 8.

DYAR (1893 *b*) has described different kinds.

*Lasiocampa rubi* L., Plate II, fig. 6, 7.

Material in alcohol of the three last instars of the caterpillars (i. e. instar *III*, *IV*, *V*), collected at Groningen, in the summer of 1913.

Instar *III*. Length 27 mm.

The whole body is covered with widely spread setae of about  $\frac{1}{2}$  mm. long. The tubercula are black, have the form of warts and possess many unfeathered setae, which are about  $1\frac{1}{2}$  mm. long.

*Prothorax*. No prothoracic shield, but there is an elevation between the three following verrucae. This elevation, however, is not black and the setae are as large as on the remaining surface of the body.

There are: *v. dorsalis*, *v. subdorsalis*, *v. suprastigmalis*, placed very high; *v. prostigmalis*, *v. basalis*, smaller *v. propedalis* and *v. postpedalis*.

*Mesothorax* and *metathorax*. *V. dorsalis* and in front of it a *verruca*, which is not coloured black and bears setae, which are about  $\frac{1}{2}$  mm. long. *V. subdorsalis*, *v. suprastigmalis*, *v. prostigmalis*, *v. basalis*.

*Abdomen* 1—9. *V. dorsalis*, *v. subdorsalis*, *v. suprastigmalis* which is placed very low; *v. prostigmalis*, *v. infrastigmalis*; *v. basalis* very large. On the fore-part of the segment *v. propedalis* is located. The proleg is coloured dark and bears setae of 1 mm. in length. All the abdominal segments bear the same pattern, with the understanding that segm. 1, 2, 7 and 8 bear a *v. pedalis* as well.

*Segm.* 10. The arrangement in my specimens is not very clear. I do not believe that there is a segment 11.

Instar *IV*. Length 33 mm. The whole body is now covered with irregularly spread verrucae between which there are also placed setae on the skin. I could not distinguish the primary verrucae. The segment is now divided into four rings. The first three especially bear the verrucae.

Instar *V* as *IV*.

Recapitulation. The third instar of the caterpillars bears a regular pattern of warts. The setae are not feathered. Between these verrucae are spread shorter setae. The pattern agrees with that of other families. There is no *v. dorsolateralis*, but we also find *v. subdorsalis* on the meso- and metathorax.

In the *IV<sup>th</sup>* instar no pattern is discernable. The number of verrucae has increased considerably. The appearance of *v. subdorsalis* on the mesothorax and metathorax may perhaps be ascribed to the same secondary augmentation of verrucae. An examination of the first two instars may possibly give an explanation of this fact.

Family *Endromidae*. FRACKER (1915) does not describe this family.

GROTE (1896) describes the verrucae as those of *Bombyx mori* instar *I*, i. e. type *I*.

PACKARD (1905, p. 40) says that the fullgrown larva of *En-*

*dromis vesiculosa* is smooth, without any hairs or only minute ones. The ontogenesis is therefore probably like that of *Bombyx mori*.

Family *Bombycidae*. The caudal horn does not resemble that of the *Ceratocampidae* according to PACKARD (1905, p. 20).

This family is to be considered as originating from the *Lasiocampidae*.

DYAR (1896b, p. 140) says that "*Bombyx mori* has true warts of the typical lasiocampid pattern".

GROTE (1896) pointed out, that the warts of instar *I* resemble those of *Endromis*.

SASAKI (1898, p. 33 sqq.) says that the dorsal horn in instar *I* is already a single median wart and this not only on *B. mori*, but also on *Theophila mandarina*, which is considered to be the primitive wild form.

PACKARD (1905, p. 40 sqq.) says that stage *I* has warts, later on the body is smooth or with minute hairs.

The genus *Ocinara* has a horn. (See i. a. HORSFIELD and MOORE).

FRACKER (1915, p. 102) says that the setae are so reduced as to be of little value in identification.

In the literature the assertion is very often met with that *Bombyx mori* is naked. It is remarkable that this species, which has been cultivated in such large quantities and is one of the few insects which have become domesticated, has been observed so insufficiently. Although indistinct, the old pattern of the verrucae remains visible to the last moment of the larval stage.

*Bombyx mori* L., Plate II, fig. 1—5.

Material in alcohol at Groningen 1914, many specimens collected every day, so that I had a very extensive collection at my disposal.

Instar *I*. Duration 40? days. Length 4 mm. The setae are not feathered, about 400  $\mu$  long. They are only placed on tubercula. Most of the swellings are verrucae with four or five setae, but *s. subdorsalis*, *s. poststigmatis*, *s. infrastigmatis* remain separately

visible. At about the time of the first moulting the *verrucae dorsales* of the abdominal segment 9 begin to stretch themselves, and rise to the "caudal horn" which reminds us somewhat of that of the *Sphingidae*.

*Prothorax.* *Verruca dorsalis* large, with four or five setae; *seta subdorsalis*, *v. suprastigmalis*, not distinctly confined, but there are three to six setae placed together; *v. prostigmalis* with three setae, *v. basalis* with three setae, *s. propedalis*, *s. postpedalis*, some small setae on the leg, and *s. ventralis*.

*Mesothorax.* *V. dorsalis* and *v. dorsolateralis* large, each with five or six setae, *s. suprastigmalis*, *v. prostigmalis* with four setae, *v. basalis* with four setae. *S. propedalis*, *s. postpedalis*, *s. ventralis*.

*Metathorax* = *mesothorax*, but sometimes there is a median dorsal seta.

*Abdomen* 1, 2. Here too this medial dorsal seta is sometimes found.

*V. dorsalis* large with four setae, *s. subdorsalis*, *v. suprastigmalis* large with four setae, *s. poststigmalis*, *s. infrastigmalis*, *v. basalis* with four setae; two or three *s. (pro- et post) pedales*; *s. ventralis*.

*Segm.* 3, 4, 5, 6 = 1 and 2, but *v. propedalis* bears two setae, and on the leg one finds at the front and the back edge two pigmental spots with one or more small setae; *s. poststigmalis* bears very often two setae, but this is not a constant feature, neither is it so on the successive segments of one individual.

" 7, 8 = 1 and 2, but *s. poststigmalis* has often been doubled.

The newly-hatched larva directly bears a *v. dorsalis* on segment 8, which is higher and larger than the other verrucae. That it is a *v. dorsalis* appears from the *s. subdorsalis*, placed behind it. The two *v. dorsales* of the right and left sides are united. When the length of the caterpillar is 4 mm. this verruca is 50—60  $\mu$ . high. It soon grows to the double height, whereas the length of the caterpillar increases only very little.

When the caterpillar is a fortnight old, it is about 6 mm. long and the *v. dorsales* have already attained a height of

about 500  $\mu$ . In other words: while the caterpillar only grows  $50\%$ , the *v. dorsales*, which soon become united, have attained a length of ten times their original one.

*Segm. 9.* *V. dorsalis* is very large with four setae, *v. suprastigmatis* is reduced to one seta; *s. subdorsalis* has disappeared, as also have *s. poststigmatis* and *s. infrastigmatis*; *v. basalis* with four setae; two setae on the ventral side I should like to call *s. propedalis* and *s. ventralis*.

" 10. *V. dorsalis* upon the anal flap with four setae, below it a very large verruca, which has possibly taken origin from a consolidation of *v. suprastigmatis* and *v. basalis* (five setae); two *s. propedales*, *s. ventrales*.

No 11th Abdominal segment can be detected.

Instar II. Duration a fortnight. Length 8 mm.

On the whole the same verrucae as in instar I, but whilst there they are distinctly confined and have dark pigments, here they consist of a small elevation of the surface, of the same colour as the rest of the body. Upon this elevation stand a number of setae, which are about 400  $\mu$  long and which therefore have not grown. The whole surface is covered by irregularly spread secondary setae, about 100  $\mu$  long and therefore distinctly contrasting to the primary ones.

*Prothorax.* *Verruca dorsalis* with five setae, *s. subdorsalis*, *s. dorsolateralis*, *v. suprastigmatis* with two setae, *v. prostigmatis*, with four setae, *v. basalis* with five setae, *s. propedalis*, *s. postpedalis*, *s. ventralis*.

*Mesothorax.* *V. dorsalis* with six setae, *v. dorsolateralis* with four setae, *v. suprastigmatis* with three small setae or already totally vanished, *v. basalis* with five setae, *s. propedalis*, *s. postpedalis*, *s. ventralis*.

*Metathorax* = *mesothorax*, but *v. suprastigmatis* has almost disappeared.

*Abdomen 1.* *V. dorsalis* with two to four setae, *s. subdorsalis*, *v. suprastigmatis* with four setae, no *v.* or *s. poststigmatis* and *infrastigmatis*, *v. (pro)pedalis* with four setae, *s. ventralis*.

*Segm.* 2 = 1, but *s. subdorsalis* is absent.

- ” 3, 4, 5, 6 = 1. but *s. subdorsalis* is absent, *v. infrastigmalis* often consists of one or two setae; and on the segments 3 and 4 there is often a *v. poststigmalis* with four setae; *v. basalis* with six setae; the pigmental spots on the leg have increased in size and bear many short setae.
- ” 7 = 1.
- ” 8. The “caudal horn” has become entirely median, and its formation by the blending of the two *v. dorsales* is no longer clearly visible. It is now 600  $\mu$  high, perhaps *s. subdorsalis* is united with it, else it has disappeared; further there occur *v. suprastigmalis* with three setae, *v. basalis* with four setae, *v. ventralis* with two setae, of which the most lateral one is perhaps *s. propedalis*.
- ” 9. *V. dorsalis* is formed by the union of the right and the left one. It is now 300  $\mu$ . high and resembles that of segment 8, but is smaller; no *s. subdorsalis*, *s. suprastigmalis*, *v. basalis* with four setae, *s. propedalis*, *s. ventralis* (see abd. 8).
- ” 10. *V. dorsalis*, with four setae; *s. subdorsalis*; one spot with setae under the anal opening, probably agreeing with *v. basalis*, *s. propedalis* and on the leg three *s. pedules*.

Instar III. Length 9 mm.

In these and the following instars all verrucae and setae remain entirely as during instar II. To prove this, I drew the abdominal segment 5 of instar V, i. e. after the last moulting (Length 40 mm.).

Distinguishable are still: *v. dorsalis*, with three setae, placed immediately beside that of the other side and behind this a black spot; *s. subdorsalis*, *v. suprastigmalis* with three setae; *v. basalis* with five setae. Further the whole leg is covered with long setae; namely more than 1000  $\mu$  long, whereas the remaining primary setae are about 500  $\mu$ ., and the secondary ones about 100  $\mu$ .. So we see that a very insignificant growth of the primary setae has taken place, namely of 400—500  $\mu$ ., whereas the body has grown from 4 to 40 mm. and during instar V to about 80 mm.

*Summary.*

In instar *I* distinct, black verrucae occur, most of them with three or four setae, some of the tubercles bear one seta and are probably already reduced, as they sometimes have two setae. The pattern on the abdomen agrees with type *I*, on the thorax with type *II*.

In instar *II* we see the secondary setae, and the verrucae are partially dissolved, but they are still visible. This is the case during all the instars of the caterpillars. The primary setae grow very little, the secondary do not grow at all, except on the abdominal legs.

The caudal horn is formed by the left and right *v. dorsales* of segment 8.

Family *Brahmaeidae*.

PACKARD (1905, p. 43) thinks that this family is the most specialized of the SYMBOMBYCINA. They have in instar *I* multisetose warts, which they lose after the first moult, as is clearly seen in *B. japonica*. PACKARD (1915, Pl. XXXIV).

In the first instars there is a caudal horn, which later on disappears. I had no material for investigation.

According to PACKARD (1893, 1905) the families we discussed just now have descended from the hairy *Notodontidae*, in particular from the *Ichthyarinae* and *Apatelodinae*. PACKARD says that in the first instar they all have warts which in a few cases they retain, but nearly always lose after instar *I*. They also agree in the pupae and imagines.

If this view is right, we have here a case of the development of setae into verrucae which, however, are soon supplanted by secondary setae. These can be very long (*Lasiocampidae*) but also very short. (*Bombycidae*).

As in the other group, the SYSSPHINGINA, a caudal horn is developed on segment 8, but here it is soft and fleshy. And as in the last mentioned group, this horn may disappear again, as is the case with the *Brahmaeidae*.

Consequently a complete parallelism exists between these groups. Of course another arrangement may also be conceived, in which the "horned" ones are placed together.

In this case, however, difficulties would be met with in regard to the warts.

The SYSSPHINGINA descend from forms (PACKARD 1905, p. 44) which bear tubercles not producing more than a single setae. The primary groups of the *Notodontidae* viz. *Notodontinae*, *Heterocampinae* and *Cerurinae* have already been discussed with the family.

Family *Ceratocampidae*. Two of the three volumes of PACKARD'S work have been devoted to this family. Of a great many caterpillars complete descriptions are given (1905—1914).

The caudal horn deserves to be specially mentioned. In *Adelocephalia* it has arisen [as is clearly visible in PACKARD'S figure, 1905, Pl. XLV, fig. 3] from the *s. dorsalis* of segment 8. It ends in two setae, exactly as in the *Sphingidae*. On the mesothorax and the metathorax too, the *s. dorsales* have increased enormously and are bifurcated. The ordinary setae change during the following instars into spinose ones, whilst the caudal horn loses the two setae at the end and then forms one single, purely median projecting part.

*Syssphinx* and *Eacles* have the same ontogenesis. In *Anisota* a median dorsal horn is developed on the metathorax from the *s. dorsales* and a median tuberculum on the 9th abdominal segment apparently from the *s. subdorsales*. *Citheronia* has many setae developed into large scoli, as well on the thoracic as on the last abdominal segments.

Except in the *Ceratocampidae* these scoli only occur on the *Hemileucidae*, the *Saturniidae*, the *Nymphalidae* and the *Heliconiidae*. PACKARD thinks with FRACKER (1915, p. 120—126) that this is of great importance and I am inclined to agree with them. It seems to me that the dorsal horn on the 8th abdominal segment too is of great importance in judging of the relationship. The number of the scoli varies greatly, secondary setae may be found or not. See FRACKER (1915, p. 121—123).

Family *Hemileucidae*. PACKARD (1914, p. 77-151, Pl. XX-XXXI).

FRACKER (1915, p. 122). The setae are partly bifurcated and situated on very long and thin tubercula, some of them bear a spinose character and are short and forked. The latter are developed from the former e. g. *Hemileuca maia*. (PACKARD, 1914, Pl. XXII).

They are arranged as on the *Saturniidae* i. e. Type Ia. *S. dorsalis* is still to be found on the abdomen of *Pseudohasis eglanterina*.

Family *Saturnidae*. WEISMANN (1876) drew attention to the spots which on the larvae are different according to their places of birth. I therefore thought it right to draw these spots in their exact shape. Plate III, fig. 14, 15.

PACKARD (1914, Pl. XXVI-XXXIII and p. 151-271). FRACKER (1915, p. 121-122). As early as in instar I the larvae have verrucae which later on become scoli. Secondary setae sometimes make the arrangement a little indistinct. Generally the scoli consist of a conical tuberculum on the top of which some (2-10) setae take their origin. The setae often end in a knob and they are glandular hairs. In the successive moults the number of setae often diminishes. On abdominal segment 8 the *sc. dorsales* are placed close together. Naked forms are also found, but the first instars have the above mentioned scoli e. g. *Rhodia fugax* (PACKARD 1914, Pl. XXVIII-XXIX). — POULTON (1890) mentions depressed scars on the pupa of *Saturnia carpina*. To me it seems that the *Hemileucidae* and the *Saturnidae* are side-branches, not directly connected with the *Sphingidae*. The description of *Saturnia pavonia* follows.

*Saturnia pavonia*. Plate III, fig. 14, 15.

Material in alcohol, cultivated at Groningen in the summer of 1915.

Instar I. Length  $3\frac{1}{2}$  mm. Head black. The tubercula are warts, mostly with 5-7 not plumed setae, which have a length of  $\pm 700 \mu$ . On the skin there are no other setae.

*Prothorax*. *V. dorsalis*, *seta subdorsalis*, *v. suprastigmalis*, *s. prostigmalis*, *v. basalis* with two setae.

*Mesothorax* and *Metathorax*. *V. dorsalis*, *v. suprastigmalis*, *v. poststigmalis*, *v. basalis* with two setae, *s. dorsolateralis*.

Abdomen 1, 2. *V. dorsalis* is the largest of the tubercula; no *v. subdorsalis*, *v. suprastigmatis* a little smaller than the other verrucae, *v. infrastigmatis* lying a little further towards the tail than usually. It may be that it has been derived from *v. poststigmatis* and *v. infrastigmatis*. Two *s. basales* close to each other and sometimes blended. Generally no *s. pedalis*.

Segm. 3, 4, 5, 6 = 1. But *v. suprastigmatis* is larger and *v. basalis* bears four setae, next to each other. On the leg is a dark spot and quite at the end is a *seta pedalis*.

" 7, 8 = 1. But *v. suprastigmatis* is about as large as the others, *v. basalis* is well developed and there is a *v. pedalis* with two or three setae.

" 9 = 1. But *v. suprastigmatis* is not clearly defined and generally bears only one long seta and two or three short ones. *V. basalis* has two setae which are sometimes separated. No distinct segment 10.

Instar II and the following instars.

All the tubercula are arranged as in instar I and grow into scoli, but *v. basalis* is dissolved into several setae, *v. pedalis* disappears. Between the verrucae setae appear on the skin directly after the first moulting. When the caterpillar is full-grown they are  $\pm \frac{1}{2}$  mm. long, (on the abdominal legs a little longer). The setae on the verrucae are  $\pm 1\frac{1}{2}$  mm., exceedingly thick and not plumed. Therefore three scoli occur on each segment: *sc. dorsalis*, *sc. suprastigmatis*, *sc. infrastigmatis*. Neither is the *s. subdorsalis* of the prothorax any longer visible.

A dark colour in the drawing of abdominal segment 5 (Plate III, fig. 15) accurately shows the spots. They do not take their origin from the primary verrucae.

Recapitulation. The pattern hardly changes. The tubercula are scoli. There is no *sc. subdorsalis* except a very much reduced one on the prothorax. Probably it has also disappeared on the other segments and for this I refer to the *Hemileucidae*. On the mesothorax and metathorax there is no *sc. dorsolateralis*. *Sc. basalis* becomes dissolved later on.

Between the scoli we see in instar *II* small setae. In instar *I* no spots, but in instar *II* we find spots along the front and back edges of the segments, they are connected with each other by a line above the stigma. Later on they are irregular.

#### Family *Sphingidae*.

WEISMANN'S important study (1876) has been mentioned before in detail. Chapter II, p. 6 sqq.

MELDOLA translated this work in 1882 and drew attention to the resemblance with the flagellate organ *Papilio* and *Dicranura* possess.

W. MÜLLER (1886, p. 250) relates among other things that the horn is composed of the two primary hairs  $1 = Ds.$  of the 8th abdominal segment and gives a drawing of it.

POULTON (1884, 1888, 1890) gave his attention to the colours of the pupae which agree with those of the caterpillars. He thinks that the horn arises from two tubercula. I intend to discuss POULTON'S opinion on the colours in the chapter on pupae.

Dr. Jur. M. C. PIEPERS published in 1889 a treatise in Dutch and in a more extensive form in German in 1897. PIEPERS, who lived for many years in the Dutch East-Indies, raised numerous *Sphingidae* from the egg. He found that the horn is very movable. [J. TH. OUDEMANS discovered the particular muscles which cause this movement]. Then he discusses the hypothesis of TH. GOOSSENS (1873) who thought that the horn serves to protect the glands by which the urine is secreted. PIEPERS thinks it is used to drive away the *Ichneumonidae* and *Tachininae*. The granulation is the consequence of a secondary disappearance of prickles so that the organ may have been a poisonous prickle formerly.

PIEPERS found also that in the beginning the horn possesses two points.

PACKARD (1890, p. 513) is remarkably short in treating this organ, but in 1905 he discusses it at length. With it he draws figures of *Ceteromia amyntor*. His Pl. XXXIV and XLII agree almost entirely with mine of *Sphinx ligustri*, in so far as there are no secondary setae except on the horn, and with *Smerinthus*

spec. as these secondary spinules are glandular setae which are bifurcated. In 1905 (p. 17—21 and p. 34—45) PACKARD worked out the relationship between the *Ceratocampidae* and the *Sphingidae*. He believed to have found a proof in the horn, which is built in a similar way, on the 8<sup>th</sup> abdominal segment.

DYAR (1894, p. 204) says only that on the 8<sup>th</sup> abdominal segment there is the dorsal tuberculum and draws attention to the position of IV and V. Tuberculum IV is placed under the stigma, tuberculum V in front of it. PACKARD (1905) follows him here, as FRACKER does in 1915.

I think there is not a single proof of a rotation of 90 degrees like that, round the stigma and I consider IV of DYAR to be in this case *s. infrastigmalis* (i. e. V) and his V as a *s. prostigmalis* i. e. as III B of Quail. Further I draw attention to the peculiar secondary setae.

I was not able to obtain FORBES' work of 1911.

*Sphinx ligustri.*

Material in alcohol. July 1915. Plate IV, figure 1.

Instar I. Length 6 mm.

*Prothorax.* There are: *s. dorsalis*, *s. subdorsalis*, *s. suprastigmalis*, *s. dorsolateralis*, two *s. prostigmales*, two *s. basales*, some small *s. pedales*. Beneath *s. subdorsalis*, at the same height as *s. dorsolateralis*, is a *s. subdorsalis inferior*.

*Mesothorax.* We find two *s. dorsales*, perhaps arisen from the blending of *s. dorsalis* and *s. subdorsalis*; *s. dorsolateralis* united with *s. suprastigmalis*, one *s. prostigmalis* in front of a wing rudiment, which at first I thought to be a rudimentary stigma, two *s. basales*, some *s. pedales* which are small.

*Metathorax* = *Mesothorax* but *s. dorsolateralis* is simple, and the wing-rudiment is not distinct.

*Abdomen* 1, 2. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmalis*, *s. prostigmalis*, *s. infrastigmalis*, *s. basalis* and ventral of it two setae probably agreeing with the *s. pedalis* and *s. ventralis*.

*Segm.* 3, 4, 5, 6 = 1. There is a *s. propedalis* and a *s. ventralis*.

" 7 = 1 but only one *s. propedalis*.

*Segm.* 8. On the place of the *s. dorsales* of the left and right sides, we find the median caudal horn which is white directly after the birth and gets black later on. The skin has totally changed on this spot and is covered with numerous, irregularly placed small setae.

I do not think that the caudal horn has exclusively been developed from the two *s. dorsales*, which are distinctly to be seen on the top, as two knobs each with a seta, but I am inclined to consider it as a protuberance which has lifted up the *s. dorsales* on its top.

Besides the horn we find in the usual order: *s. subdorsalis*, *s. suprastigmatis*, *s. prostigmatis*, *s. infrastigmatis*, *s. basalis*, and *s. propedalis*.

" 9 = 1. But *s. infrastigmatis* is absent, there is only one *s. basalis* and one *s. propedalis*.

" 10. *S. dorsalis*, *s. subdorsalis* and *s. suprastigmatis* on the anal-flap; there is a *s. prostigmatis*, *s. infrastigmatis* is absent, one *s. pedalis*.

" 11. Just under the anal-flap a large tuberculum with setae. The seta under it we might take as *s. basalis* of segment 10, but in connection with the reduced number of setae of segment 9, this does not seem probable to me. I consider this tuberculum to belong to the ventral part of 11.

Instar *II* and the following instars.

The primary tubercula and setae have disappeared. The skin is totally covered with small tubercula placed in vertical rows, each of which has a very short seta.

Recapitulation. Instar *I* has a primitive setal-pattern, which is nearly the same as that of the other families. The caudal horn has arisen on the place of the left and right *setae dorsales* which remain visible on the top. With some exceptions (meso- and meta-thorax) which it is easy to explain, the tubercula bear one seta.

There is no *s. poststigmatis*, but we find on the abdominal segment a *s. prostigmatis*. In instar *II* this pattern is lost and

then the caterpillar acquires secondary setae which are so short and homogeneous that it seems to be naked.

*Smerinthus tiliae.*

Material in alcohol. July 1915. Plate IV, Fig. 2a, b.

Instar I. Length 3 mm.

The head is very large. Besides the tubereula described below, the whole body and the caudal horn too, are covered with irregularly placed small setae, the length of which is  $\pm 50 \mu$ . With a low power it looks as if they are bifurcated at the end as has been figured by SHARP (II, p. 359) for instar I of *Euchloe cardamines* and by PACKARD (1905) for that of *Ceteromia amyntor*. Highly magnified they appear to consist of a couple of bigger rays and a number of thinner ones, all protruding from the upper part of the seta. The whole thing might be compared with an umbrella turned upside down of which some of the ribs are thicker than the other. Plate IV, fig. 2a.

The primary tubereula are not black in reality: the black in the figure is only intended to draw attention to them.

*Prothorax.* There are *s. dorsalis*, *s. subdorsalis*, *s. suprastigmalis* or *s. dorsolateralis*, as it stands a little lower than one might expect at first sight, *s. prostigmalis* and *s. infrastigmalis*, two *s. basales* placed next to each other, some smaller *s. pedales*.

*Mesothorax* and *Metathorax.* *S. dorsalis*, *s. suprastigmalis* or *s. dorsolateralis*, *s. prostigmalis*, two *s. basales*, a few smaller *s. pedales*.

*Abdomen* 1. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmalis*, *s. prostigmalis*, *s. infrastigmalis*, two *s. basales*, one of which agrees with *s. pedalis*.

*Segm.* 2 = 1. One *s. basalis*.

„ 3, 4, 5, 6. 7 = 2 i. e. one *s. basalis* and one *s. pedalis*.

„ 8. We must consider the caudal horn as in the case of *Sphinx ligustri*. The skin is continued in unaltered condition over the horn and bears the same umbrella-shaped setae, for the rest as with 2.

*Segm.* 9 = 2, but *s. infrastigmalis* fails.

- " 10. *S. dorsalis*, *s. subdorsalis* and *s. suprastigmalis* on the anal flap, under it *s. prostigmalis*; *s. infrastigmalis* is absent, one *s. pedalis*.
- " 11. Behind the anal flap is one tuberculum belonging to the dorsal part of segment 11.

Instar *II*. The pattern described above is totally absent here. The skin is covered with the tubercula described for *Sphinx ligustri*.

Recapitulation. The setal pattern of instar *I* quite agrees with that of *Sphinx ligustri*, only the *s. dorsolaterales* or the *s. suprastigmatales* on the thoracic segments are wanting.

The caudal horn just as in *Sphinx ligustri* originates by a median protuberance of abd. *segm.* 8 under the left and right *s. dorsales*.

Between these primary tubercula we find small umbrella-shaped setae.

In instar *II* this whole pattern has disappeared just as the particular setae which have been replaced by small ones of the ordinary form.

### *Smerinthus populi* Linn.

Material on alcohol. July 1914. Plate IV, fig. 3a, b.

Instar *I*. Length 4 mm.

The whole surface is covered with the small umbrella-shaped setae, which I described for *Smerinthus tiliae*. The primary tubercula and setae are wanting except:

*Prothorax.* *S. infrastigmalis*, one *s. basalis*.

*Mesothorax* and *metathorax.* One *s. basalis*.

*Abdomen* 2. *S. infrastigmalis*, *s. basalis*, *s. pedalis*.

*Segm.* 3, 4, 5, 6. *S. basalis*, *s. pedalis*.

- " 8. The caudal horn bears no other setae but the umbrella-shaped ones, and is very short. Further one *s. basalis*, just as on 9 and 10.

Instar *II*. We only find the small tubercula and setae described for *Smerinthus tiliae* and *Sphinx ligustri*.

Recapitulation. The homogeneous setae together with the umbrella-shaped ones, which in *Smerinthus tiliae* are found by the side of the primary pattern, have almost entirely replaced the old pattern in instar *I*. In instar *II* it is replaced by short setae.

*Pterogon proserpina* Pall. and *P. gorgoniudes* Hb. in the collection KALLENBACH are homogeneous in the two last stages and are covered with thin and small setae.

*Macroglossa stellatarum* L., *M. croatica* Esp., *Hemaris scabiosae* Z. and *H. fuciformis* which are all in the collection KALL. as the last instar of caterpillars, are naked.

Family *Lithosiidae*. The setae and verrucae are arranged according to type **I**, the same as in *Arctiidae*.

FRACKER (1915, p. 118) saw no other species than those with setae instead of verrucae. This family is therefore probably rather primitive. *Rho* on the abdomen and *Pi* on the mesothorax and metathorax are double and from this FRACKER concludes the reduction of the verrucae to setae.

The collection KALL. had no material for investigation.

Family *Arctiidae*. In this family the arrangement of the verrucae is very distinct, so that DYAR (1894) gave the name of Aretian type to an arrangement which almost completely agrees with Type **I**.

FRACKER (1915, p. 114—118) gives a table of genera with which he himself is not satisfied.

This writer thinks that the genera *Doa* and *Utetheisa* are reduced, as they only bear setae and no verrucae. I might add *Hipocrita* (*Euchelia*) but think that this condition should rather be considered as something primitive.

To prove his opinion he says (discussing the *Noctuidae*, l. c. p. 113) that *Doa* possesses a multisetiferous leg-plate and that the *Pi*-group on the metathorax of *Utetheisa* is bisetose.

I am not convinced by these arguments, as the setae on the legs of primitive caterpillars are often numerous and the thorax in general often bears two *s. basales*.

*Hipocrita (Euchelia) jacobaea* Linn.

Material 1915 (the Hague) and coll. KALL. Plate IV, fig. 7.

The specimens collected by me in the middle of April measured 10 mm. I did not succeed in cultivating them, therefore I do not know to which instar they belonged. The arrangement of the setae of these specimens is the same as of those of coll. KALL. The full-grown specimens are 35 mm.

*Prothorax.* *S. dorsalis*, *s. subdorsalis*, *s. prostigmalis*, two *s. basales* on one tuberculum, *s. propedalis*, *s. postpedalis*.

*Mesothorax* and *Metathorax.* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmalis*, *s. prostigmalis* and on the place of the wing-rudiment one seta. One might be tempted to look for the rudimentary stigma on this spot, as in this place the air-tubes arise from the main trachea. Two *s. basales*, *s. propedalis*, *s. postpedalis*.

*Abdomen* 1, 2. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmalis*, *s. poststigmalis*, *s. infrastigmalis*, two *s. basales* on one tuberculum, *s. pedalis*.

*Segm.* 3, 4, 5, 6 = 1, but instead of *s. pedalis* there is a seta on the front side of the leg = *s. propedalis*.

" 7, 8, 9 = 1.

" 10 = 1, but somewhat reduced, for *s. poststigmalis* and *s. infrastigmalis* are absent. On the anal legs three setae.

*Pupa.* Coll. KALL. no setae.

*Arctia caja* Linn. Plate IV, fig. 4, 5 a, b.

Material on alcohol. Groningen 1914.

Instar *I.* Length 6—7 mm. The head is black, the tubercula are brown, they soon begin to colour. The tubercula are warts, the setae are plumed.

*Prothorax.* There is no prothoracic shield, but the two *v. dorsales* of the left and right sides approach one another and they have progressed a great deal over the segment in ventral direction. *V. subdorsalis* is very small. *V. suprastigmalis* is large and situated a little lower than usually is the case in other families of cater-

pillars. There is also a large *v. basalis*, and some non-plumed setae on the leg.

*Mesothorax* and *metathorax*. We find *v. dorsalis*, *v. suprastigmatis* and *v. prostigmatis* which are about equally large. The last mentioned wart lies on the same height as the very high placed *v. poststigmatis* on the abdominal segments. *V. dorsolateralis* is wanting.

Behind *v. prostigmatis* is a small tuberculum with three or four setae. It lies therefore on the place of the wing-rudiment. Besides we find in many individuals a tuberculum with one or two setae.

*V. basalis* is large. On the leg occur some setae which are not feathered.

*Abdomen* 1, 2. *V. dorsalis* is a little smaller than *v. subdorsalis*, *v. suprastigmatis* is large. Large and far projecting is *v. poststigmatis* which is partly continued under the stigma towards the head. *V. infrastigmatis* is situated lower than in most of the other families of caterpillars. *V. basalis* and *v. pedalis* on the place where on the abdominal segments the leg is fixed.

*Segm.* 3, 4, 5, 6 = 1, except that *v. pedalis* is absent. But on the leg are one or two strong setae.

" 7, 8 = 1.

" 9. Very small *v. dorsalis*, very large *v. subdorsalis* which has far extended in the direction of the missing *v. suprastigmatis*, this being perhaps united with it. For the rest as 3. Moreover there is a rather large tuberculum under the anal flap. I consider this to be *v. infrastigmatis* of *segm.* 10.

Consequently the 10th segment is very much reduced.

*Instar II.* Duration 30 days. Length 12 mm.

The whole animal looks exactly as in *instar I*, but between the tubercula a few setae (generally not plumed) are found.

*Prothorax.* *V. dorsalis* is still larger than in *instar I* and *v. subdorsalis* too has grown longer. Under it is a new verruca. For the rest as in *instar I*.

On the abdominal segments we see some small tubercula in the neighbourhood of *v. infrastigmatis*. *V. poststigmatis* now grows

nearly entirely under the stigma so that the following warts are lying almost in one line, which also passes through the stigma and the middle of the leg. *V. dorsalis*, *v. suprastigmalis*, *v. poststigmalis*, *v. infrastigmalis* and *v. basalis*.

The other instars remain unchanged.

Recapitulation. The wart-shaped tubercula bear in all instars plumed setae. The pattern (Type I) is very simple and hardly changes during the different instars. All the different tubercula are about equally large.

There is no *v. dorsolateralis*. *V. poststigmalis* is shifted a little under the stigma, *v. infrastigmalis* is situated on a low level.

*Spilosoma (Ocnogyne) lubricipeda* Linn. Plate IV, fig. 6.

Entirely as *Arctia caja*, but in the beginning the setae are not feathered. *V. poststigmalis* is also shifted from under the stigma. The setae on the leg are very densely feathered. On the ventral side mediad of the leg a tuberculum without setae = *v. centralis* occurs.

In instar IV a linea dorsalis is present.

Family *Syntomidae*. The verrucae completely agree with type I, but there is only one verruca on the mesothorax and metathorax over *v. prostigmalis*. This only occurs in the *Pericopidae*. The verrucae change a great deal in form, size and number. FRACKER (1915, p. 118) found that segment 7 has the same pattern as the other abdominal segments. The setae are plumed and often form pencils. Mostly secondary setae.

Coll. KALL. no material.

Family *Nolidae*. FRACKER puts this family (1915, p. 98) with the *Lacosomidae* as *Microlepidoptera* of uncertain position after the ZYGAENOID series. The caterpillars bear verrucae which remind us of those of the *Arctiidae*.

Family *Agaristidae*. FRACKER (1915, p. 114) examined different kinds and comes to the conclusion, that it is right to unite this family with the *Noctuidae*. This harmonizes with the fact that HANDLIRSCH (1908) places these families close together.

Coll. KALL. no material.

Family *Noctuidae*. Whilst PACKARD (1895, p. 83) entirely separated this family from the *Bombyces*, he says (1905, p. 41) "that in the SYMBOMBYCINAE the noctuiform characters are crowded back in the phylogeny of the group."

DYAR (1899) describes some *Hydrocciae* and proves the existence of a large *s. prostigmalis*.

FRACKER (1915) devotes some pages (p. 111—118) to the owl-moths and describes the difficulties he met with.

He divides the family into four groups, "they are, however, purely for convenience and do not constitute a natural arrangement." His groups are:

I. Larvae with primary setae only. The pattern agrees with that of *Mamestra* and *Depressaria* (see below).

To this not a single *Acronycta* species belongs, otherwise the greater part of the genera.

II. Larvae with well developed verrucae, arranged as in *Arctiidae* but  $\alpha$  (*v. prostigmalis*) is often small and on segment 7 it stands on a lower level than on 6 and 8. To these belong the *Acronyctinae* in part.

III. Larvae with verrucae which are obscured by the development of secondary setae. *Acronycta* in part.

IV. Verrucae reduced to single setae, although preceeded by well developed tufts in earlier stages;  $\mu$  (= *v. basalis*) remains present as verruca, which is very peculiar as a proof of the pseudo-primitive character. *Acronycta* in part.

FRACKER (1915, Pl. III and IV) also describes *Feltia glandaria* instar I and full-fed. We find here the following peculiarities:

a. instar I has no *s. infrastigmalis* ( $\nu$ ) on the prothorax, though we do find it on the full-grown form.

b. instar I has no *s. prostigmalis* ( $\epsilon$ ) on the abdomen, but gets one in maturity.

In the last case, supposing it really has been stated rightly, I presume that FRACKER's labeling is not correct. For then the seta on the abdomen is either subprimary or secondary and on the thorax he calls it a primary seta, whilst he says on p. 21

that it is not allowed to homologize a primary with a secondary seta. The many caterpillars in the coll. KALL. agree with FRACKER'S groups. As examples of the 4th group I mention *Acronycta alni*, where the *s. subdorsales* reach a great length and *Diloba coeruleocephala* L.

I should like to propose a 5th group viz.:

V. The setae or the verrucae have disappeared, the pigmental spots on the tubercula remain. e.g. *Nonagria (Depressaria) nervosa*. Coll. KALL. Pl. IV, fig. 10.

*Mamestra brassicae* Linn.

This species belongs to group I. Plate IV, fig. 8 a, b.

*Prothorax.* *S. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. prostigmatis*, three *s. basales*, *s. propedalis*, *s. postpedalis*, *s. ventralis*.

*Mesothorax* and *Metathorax.* *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis*, *s. prostigmatis*, *s. poststigmatis*, two *s. basales*, *s. propedalis*, *s. postpedalis*, *s. ventralis*.

*Abdomen.* 1—9. *S. dorsalis*, *s. dorsolateralis*, *s. suprastigmatis*, *s. prostigmatis* (very small); *s. poststigmatis*, *s. infrastigmatis*, two *s. basales*, *s. propedalis*, *s. ventralis*, some *setae pedales* which are also developed in 1, 2, 7, 8, 9.

It is therefore quite like type I.

*Acronycta psi* Linn. Plate IV, fig. 9 a, b.

I only want to draw attention to the following segments which, side by side of the verrucae I am going to mention, also have secondary setae, especially on the ventral half.

*Metathorax.* *V. dorsalis*, *v. dorsolateralis*, *v. suprastigmatis*, some *s. prostigmatis*, *v. basalis*, some *s. propedales*.

*Abdomen* 1. *V. dorsalis* has grown enormously and has blended with that of the other side to a fleshy stump. *V. subdorsalis* small, but still recognisable, *v. suprastigmatis*, *s. prostigmatis*, *s. basales*, *v. pedalis*.

*Segm.* 2 = 1, but without a horn, *v. dorsalis* is smaller than *v. subdorsalis*.

„ *S. V. dorsalis*, *v. subdorsalis*, (united with that of the other

side to a fleshy horn) *v. suprastigmalis*, *v. prostigmalis*, two *s. poststigmatales*, some *s. basales*.

The caudal horn has in this case taken origin from *v. subdorsalis*, in the *Sphingidae* on the contrary from *v. dorsalis*, this is a morphological proof of the fact that these horns are not homologous.

Family *Brephidae*. FRACKER (1915, p. 101) ranges *Brephos* etc. with the *Geometridae*. The presence of the first three pairs of ventral legs, even if they have become rudimentary, seems to me to be of sufficient importance to make this group a family apart.

Family *Epiplemidae*. FRACKER (1915, p. 100) gives a normal setal type, with the *s. poststigmatales* and *s. infrastigmatales* placed close together on some segments.

Family *Geometridae*. FRACKER (1915) only says that this family of the loopers or inch-worms differs very much in armature, setae etc. In the coll. KALL. there are only full-grown specimens (e. g. *Abraxas grossulariata*, *Amphidasis betularia*), to my regret, as I should like to examine first instars.

The setae are placed on the mesothorax and metathorax according to type II, on the abdomen according to type I. There is, however, a *s. subdorsalis inferior* and *s. suprastigmatales* is placed a little more caudal than usually.

Family *Cymatophoridae*. SPULER figures these caterpillars as quite naked, but probably small setae are present. FRACKER (1915) unites the three following families, founded on the investigations of BUSCK and WALSINGHAM, to the PYRALOID series of the MICROLEPIDOPTERA-NONACULEATA; HANDLIRSCH (1908) on the other hand puts these families just in front of the *Thyrididae* and *Hesperidae*, as the nearest relatives of the *Papilionidae* s. l.

I think that the verrucae which do not occur in other *Microlepidoptera*, point to a considerable difference, though I must acknowledge that in several families verrucae arise from setae.

Family *Pyralidae*.

DYAR (1894) described the *Pyralidina* as Generalized Frenatae with the tubercula IV and V (i. e. *s. poststigmatales* and *s. infrastigmatales*) approximated and single haired.

In 1895 he referred to it again and added: I and II i. e. *s. dorsalis*, *s. subdorsalis* remote, (opposed to I and II consolidated: *Arthrocerina*).

CHAPMAN (1896) thought that the *Pyraloids* belong to *Tineina* with obsolete pupae.

HOFMANN (1898) thought that the *Pyralidae* like the *Tineidae* etc. remain primary.

FRACKER (1915) says: *Kappa* is bisetose on prothorax and there is a close association of  $\kappa$  and  $\eta$  on the abdomen; (i. e. *s. post-stigmatis* and *s. infrastigmatis*). With the different genera there is some dissimilarity in  $\Pi$  (*s. basales*), but further the distinction on p. 87—94 is made by other characteristics than the setae.

Family *Orneodidae*. *Kappa*- and  $\Pi$ -groups bisetose (FRACKER 1915, p. 94), for the rest as the former family.

Family *Pterophoridae*.

DYAR (1894) states that tuberculum I = *v. dorsalis* is absent, and the tubercula are many-haired.

In 1895 he says that I and II are consolidated.

CHAPMAN (1896) figures some *Pterophoridae*, but adds that the hairs have been represented rather too diagrammatically. He says on p. 135: "As regards its panoply of hairs, spines, bristles and other appendages, the different species of *Pterophorus* present immense variety, some being very smooth and plain and with a delicate shell, others most elaborately clothed with hairs and spines of various arrangements."

QUAIL (1904) says that the trapezoid tubercles (*s. dorsales* and *s. subdorsales*) do not only occur on the abdomen, but also on the thorax, just as in the *Hepialidae*.

FRACKER (1915) does not mention any literature and says on p. 94 "that the prolegs are long and stemlike. No other caterpillars possessing verrucae and secondary setae have prolegs of this shape, although a few lower micros with primary setae show similar structures. All of the latter, however, have a trisetose *Kappa*-group on the prothorax, while that of the *Pterophoridae* is bisetose as in other *Pyraloidae*".

O. HOFMANN (1898) wrote an excellent article on this family, with twelve figures.

Having no material for independent investigation, I quote HOFMANN as follows — from which we see that in this well defined, natural family much difference occurs in the pattern, though it shows the fundamental type I. —

*Tueniocampa gothica* L. (l. c. fig. 1, 2) has on the abdomen: *s. dorsalis* (I), *s. subdorsalis* (II), *s. suprastigmatis* (III), *s. poststigmatis* (IV), *s. infrastigmatis* (V), *s. pedalis* (VII) and on the mesothorax: I—IV in an oblique row as mentioned before. I probably would not label them in this way. I take V as *s. prostigmatis*, VI then is *s. infrastigmatis*, VII = *s. pedalis*.

*Eucnemidophorus rhododactylus* S. V., (l. c. fig. 4) has on the abdomen:

*s. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. infrastigmatis*, *s. poststigmatis*, *s. basalis*, two *s. pedales*.

*Platyptilia gonodactyla* S. V. (l. c. fig. 8) almost entirely agrees with it, but here, as DYAR would have it for all *Pterophoridae*, *s. infrastigmatis* is placed on the same tuberculum as *s. poststigmatis*. Between these setae and the two *s. pedales* there are three *s. basales* of which two are placed higher than the third.

*Pterophorus monodactylus* L. (l. c. fig. 12) resembles it very closely but VI (i. e. *s. basalis*) is absent.

*Leioptilus curphodactylus* Hb. var. *buphthalmi* Hfm. (l. c. fig. 6) agrees with *Leioptilus distinctus* H. S. (l. c. fig. 9), through the possession of a secondary seta over the stigma. Therefore we might describe this pattern: *s. dorsalis*, *s. infrastigmatis*, *s. subdorsalis sup.* and *inf.* The last-mentioned species has, moreover, one more seta under the stigma, whilst IV and V are not united.

*Aciptilia tetradactyla* L. (l. c. fig. 5) has verrucae, but a secondary seta *subdorsalis inf.*

On *Oxyptilus leonari* Stange (l. c. fig. 7) on the other hand, I and II are united to one verruca.

*Platyptilia gonodactyla* S. V. (l. c. fig. 11) bears on the mesothorax: I + II or according to my view two *s. dorsales*;

III + IV or two *s. suprastigmatales*, perhaps *s. dorsolateralis* is united with I or III, V is doubled with a secondary seta = *s. prostigmatales*, moreover a secondary seta over the wing-rudiment; two *s. basales*, *s. pedalis*.

*Stenoptilia peliodactyla* Stein (l. c. fig. 10) agrees with it in so far as I + II together form a verruca, as also do III and IV. There is moreover a secondary verruca over the wing-rudiment.

I do not understand why we are to accept a doubling for V and a consolidation for I + II.

In both cases there are two setae in the place where usually there is one; if one couple is interpreted as a consolidation, the same ought to be done for the other.

#### Family *Thyrididae*.

The place of this family seems to be very uncertain. PACKARD considered it in 1895 as a very primitive side-branch of the *Neolepidoptera* far from the *Bombycina* (p. 83) but in 1905 (p. 46) he could derive the *Notodontidae* directly from them.

SHARP places it (1901, II) between the *Megalopygidae* and the *Lasiocampidae* which last group he sharply separates from the *Bombyces*, whilst FRACKER (1915) ranges it between the *Liparidae* and the *Notodontidae*. HANDLIRSCH thinks that its place is just in front of *Hesperidae* and *Papilionidae* s. l. together with the *Pyralidae*, *Pterophoridae* and *Orneonidae*.

This short account which might be enlarged a great deal, shows at least that the family has a rather primitive character.

In the coll. KALL. is a beautiful, full-grown specimen of *Thyris fenestrella* of which the drawing is to be found on Pl. IV, fig. 11, 12, 13.

#### *Thyris fenestrella* Linn.

*Prothorax*. A paired prothoracic shield with *s. dorsalis*, *s. subdorsalis*, *s. suprastigmatales*, two *s. prostigmatales*, of which the last is perhaps *s. infrastigmatales*, two *s. basales* on one tubercle, *s. propedalis*, *s. postpedalis* and one median *s. ventralis*.

*Mesothorax* and *metathorax*. *S. dorsalis*, *s. dorsolateralis* together with *s. suprastigmatales* on one tubercle, on the place of *s. pro-*

*stigmatis* a black spot without a seta, *s. poststigmatis*, *s. infrastigmatis*, two *s. basales* on one tubercle, *s. propedalis*, *s. postpedalis* or *s. ventralis*.

On the *metathorax* a small seta only on the left side on the place for *s. subdorsalis* occurs. Where there are no other secondary setae on the caterpillar, I think, I may conclude that *s. subdorsalis* in other cases has disappeared from the thorax. A remnant like that might be expected in the first place in a primitive animal. On the *mesothorax* is a black spot in front of the *s. basales*.

*Abdomen* 1. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. infrastigmatis*, two *s. basales* on one tubercle, between these and the others a black spot without a seta, *s. pedalis*, *s. ventralis*. (In connection with the pattern of the *Tineidae* it is not quite improbable that the seta under the stigma agrees with *s. poststigmatis* and that the black spot represents the vanished *s. infrastigmatis*. I prefer, however, not to bring hypothetical suppositions like these to expression in nomenclature).

*Segm.* 2 = 1, but between the *s. basales* and *s. pedalis* is another seta = *s. propedalis*(?)

„ 3, 4 = 2, but the black spot under *s. infrastigmatis* is wanting and next to the already mentioned *s. propedalis* we find on the base of the leg two *s. pedales* and also *s. ventralis*.

„ 5, 6 = 3, but *s. propedalis* of *segm.* 2 is double, the *s. pedales* are placed on the outside of the leg, and *s. basalis* is not doubled.

„ 7 = 2, but *s. propedalis* is double and *s. basalis* single.

„ 8 = 2, but *s. basalis* is single.

„ 9 = 2, but the *s. dorsales* and the *s. subdorsales* from the left and right sides are situated on a median dorsal shield, *s. basalis* is single.

„ 10. On the anal shield we find *s. dorsalis*, *s. subdorsalis*, *s. suprastigmatis* from the left and right sides, further *s. infrastigmatis*, *s. basalis*, *s. pedalis*, *s. ventralis* are present.

There is no trace of an 11<sup>th</sup> segment.

Family *Aegeriidae* (= *Sesiidae*). This family shows a certain relationship with the *Sphingidae*.

In BEUTENMÜLLER'S enormous work (1900) DYAR has described the caterpillars. FRACKER (1915) adopts these results with some modifications. DYAR says (p. 228) that all the tubercles are single, there never being any development of warts or secondary hairs. The abdomen has type I with *s. poststigmatis* and *s. infrastigmatis* united.

It is the same on the *prothorax*, but there is a *s. subdorsalis inf.*, and *cerruca suprastigmatis* and *c. prostigmatis* each bear three setae, the two *s. basales* are on one tuberculum.

*Mesothorax* and *Metathorax* according to DYAR: "I<sup>a</sup> and I<sup>b</sup> united, II<sup>a</sup> and II<sup>b</sup> likewise, but IV and V well separated, IV being even nearer to III than to V, a curious circumstance".

I think there are: *s. dorsalis* + *s. dorsolateralis*, *s. suprastigmatis* + *s. prostigmatis*, *s. poststigmatis*, *s. infrastigmatis*, *s. basalis*, *s. pedalis*.

### Rhopalocera.

FRACKER believes that the butterflies arose from the *Microlepidoptera* in a time when  $\alpha$  and  $\gamma$  had not yet become adjacent.

Family *Hesperiidae*. No material in the coll. KALL.

FRACKER (1915, p. 127) follows the descriptions of SCUDDER (1889) not only in this family but in all the *Rhopalocera*.

This family deviates a great deal from the others which HANDLIRSCH takes together under the name of *Papilionidae* s. l.

FRACKER says: "Secondary setae numerous, small flattened plates sometimes present, possibly showing position of primary setae, setae on the head often plumose."

Family *Megathymidae* with the last-mentioned one united to the *Hesperioidae*.

FRACKER (1915, p. 128) says, "no setae on dorsal half, numerous on ventral half of the first two thoracic segments, rare or absent on abdomen except prolegs."

Family *Lycaenidae*. These larvae resemble ZYGAENOIDEA a little (FRACKER 1915, p. 128).

There are many secondary setae, sometimes in tufts or pencils.

It seems to me that as full-fed larvae most kinds possess a homogeneous distribution of the setae.

The verrucae of *Thestor ballus* F. (coll. KALL.) I consider to be *v. dorsalis*, *v. infrastigmalis*, *v. basalis*.

#### Family Pieridae.

Although these insects are very numerous and have long served for investigations (even SWAMMERDAM directed his attention to *P. brassicae*), still opinions differ a great deal concerning them.

J. F. VAN BEMMELEN confined himself in 1912 to a comparison between the pattern of a full-grown caterpillar of *P. brassicae* and the pupae of various *Pieridae*, *Vanessa* spec. and *Papilionidae* and found patterns which harmonized fairly well (compare chap. III and VII).

FORBES (1910?) thinks, according to FRACKER (p. 136) that the chalazae — large spots bearing the setae — have come from primary hairs.

FRACKER (1915, p. 136) denies this.

BUCKLER (1886, Part I p. 148 sqq. Pl. II sqq.) gives long descriptions of various *Pieridae*, with illustrations of different instars.

Very conspicuous is on Pl. III fig. 1b. *P. daplidice*, which also by HÜBNER (1786, Vol. I) has been represented as possessing a setal pattern just like that of *P. brassicae* in instar I.

The only one, who as far as I know, has occupied himself with a similar investigation about the ontogenesis of the chalazae, is FROHAWK (1914). It is a pity that this careful study will probably be unattainable for most entomologists.

FROHAWK also draws this caterpillar, but in the last instar substitutes this primary pattern by a homogeneous distribution of the setae. Probably the first-mentioned writers have studied a younger instar or otherwise have met with deviating individuals keeping the old pattern.

HORSFIELD and MOORE give (1857, Vol. I, Pl. I, fig. 13, 14) a similar drawing of *Pieris eucharis* Drury and *P. belisama* Cramer.

SHARP gives (1901, II p. 358) a drawing of *Euchloe cardamines* instar I with bifurcated glandular hairs in the primitive arrange-

ment, later on the *s. dorsales* only remain in existence in an unaltered condition.

*P. dapidice* also possesses these glandular setae.

QUAIL (1904) discovered III B = *s. prostigmalis* on *P. brassicae*.

In opposition with these opinions we find others e. g.:

PACKARD (1890, p. 495). "The true *Pierinae* all live on herbs, sometimes on low bushes and none of them is provided with hairs, bristles or spinules."

DYAR (1894, p. 204) says: no trace of tubercles.

DIXEY (1894) devoted an article to the phylogeny of the *Pierinae*, paying attention to the wings only. It would be very interesting to repeat this study for the larvae.

As it seemed important to me to examine this question closer, I chose the caterpillars of two kinds, which are often found on the same plant (*Brassica*), and are very similar as egg and as imago, but of which one bears bright warning colours (POULTON, 1890) and the other is in near accordance with the surroundings (protective coloration).

*Pieris brassicae* Linn. Plate V, fig. 1—7.

Material. Eggs and larvae of the 2<sup>nd</sup> generation, laid on cabbage and *Tropaeolum*.

Eggs laid in groups on the lower side of leaves, 1 mm. high, shape of a pitcher, with 15—18 (mostly 18) vertical ribs, cross-striped. The head of the larva can be seen at the side during the last two days. Duration 4—6 days.

Instar I. Duration 4 days. Length 2½ mm. The larvae bite a little hole in the side of the egg-shell, eat the top of the egg and crawl out. Then they eat the whole egg-shell. Tubercula black, skin yellow-green, transparent, no trace of stripes. Head immediately black, at first a little transparent, after ten minutes pitch-black. Setae near the eyes.

*Prothorax*. There occur: *s. dorsalis*, *s. subdorsalis*, *s. suprastigmalis*, two *s. dorsolaterales* on one tuberculum, a minute *s. prostigmalis*, mostly two *s. basales*.

The prothoracic shield appears half an hour or two hours

after the hatching, a fact which deserves attention as the head and the tubercles are black from the beginning.

*Mesothorax* and *Metathorax*. *S. dorsalis*, *s. suprastigmatis*, *s. dorsolateralis*, a small *s. prostigmatis*, no rudimentary stigma, though the tracheae are seen through the skin; *s. basalis*, sometimes a *s. pedalis*.

On the border of the mesothorax and metathorax is a rudimentary stigma.

*Abdomen* 1, 2. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. poststigmatis*, *s. infrastigmatis*, three *s. basales*.

Even after repeated examination I could not find in my material a *s. prostigmatis*.

*Segm.* 3—6 = 1, but two *s. basales* on one tuberculum.

„ 7 = 1, two *s. basales*.

„ 8 = 1, two *s. basales*, large stigma.

„ 9 = 1, no *s. infrastigmatis*, in the beginning a rudimentary stigma(?).

„ 10. *S. dorsalis*, *s. subdorsalis* and *s. suprastigmatis* with that of the other side on one median anal shield which gets black from half an hour to two hours after the hatching, whilst the tubercles are immediately black, two *s. basales*, rather far from each other.

„ 11. Behind the anal shield is a black spot with a single seta. I think that a part of the *s. basales* of 10 belongs to 11, as *s. infrastigmatis* fails already on 9.

Towards the time of moulting brown-red spots appear between the primary setae, which are mostly ring-shaped. They also arise as a broad border round the primary tubercles, and are due to the transparency of the skin which allows the colours of instar *II* to be visible.

Instar *II*. Length 4 mm.. Duration 4 days. The skin bursts just behind the head. The caterpillar creeps out at the front, as when leaving a bag, the skin of the head remains for a short time as a shield on the head. The caterpillar does not eat the old skin.

In the middle of the back we see a rather sharply confined,

bright-yellow *linea dorsalis*, beginning between the two prothoracic shields and ending near the anal shield; the skin is green. The arrangement of the tubercula is as in instar *I*, but the setae are much longer and between the primary ones numerous small, secondary tubercula, each with one seta, have inserted themselves.

The prothoracic shield has now four tubercula, one ventrad of *s. subdorsalis* has been added = *s. subdorsalis inf.*?

On the distal border is a row of red spots. On all the segments the easily recognisable primary tubercula are round the edges still a little red. Segment 11 is no longer to be seen distinctly.

Instar *III*. Length 6—8 mm. Duration 4—5 days.

Besides the characteristics of instar *II*, we see a bright-yellow *linea stigmalis* and many small hairs between the primary ones which remain distinctly visible. Instead of the mono- and bisetose tubercula basalia we find on the segments 3—6 a row of *s. basales*, curving over the beginning of the abdominal legs and over the places where legs might have stood on the segments 1, 2, 7, 8.

On the abdominal and anal legs there is a black spot covered with short hairs, which spot might perhaps be taken as a highly modified *s. pedalis*.

Instar *IV*. Length 12 mm. Duration 5 days.

The smaller setae have grown a great deal, especially one under *s. subdorsalis* of the abdominal segments. Between *s. dorsalis* and *s. suprastigmalis* on one side and *s. subdorsalis* on the other we see a new distinct row and also one spot caudal of *s. subdorsalis*.

We can easily recognize the primary tubercula: *s. dorsolateralis* of the prothorax for instance is double as in instar *I*.

They nearly all possess, however, a ring of smaller setae round the larger ones. The stigmal line gets very broad.

Instar *V*. Length 23 mm. (to 45 mm.) Duration 9—14 days.

The tubercula are very large and conical, they bear many setae (= chalazae).

The *linea stigmalis* is continued on the head as a white stripe. The arrangement of newly arisen tubercula in vertical rows is

distinctly visible. On the meso- and metathorax *chal. dorsalis*, *chal. dorsolateralis* and *chal. suprastigmatis* are united.

We can still recognize the primary tubercula on the abdominal segments, though *chal. suprastigmatis* has become double. The arrangement in cross-rows is more striking than that in horizontal ones. Distinct are e. g. on abd. segment 5: *chal. dorsalis*, *chal. subdorsalis*, a double *chal. suprastigmatis* (oral of it a large tubercle), *s. poststigmatis* and *s. infrastigmatis*. Many *s. basales*, and under *chal. subdorsalis* a large new chalaza.

Instar *VI* = *Chrysalis*. As J. F. VAN BEMMELEN (1912, p. 114 and fig. 6) has shown, we can compare the spots of the pupa with the chalazae of the caterpillars.

This is especially clear when the stigmata are examined. I feel justified in designating the spots as follows: the spot under the stigma as *macula infrastigmatis*, that behind it as *m. poststigmatis* and taking this for granted, the lowest of the four spots over the stigma as *m. suprastigmatis*. I see the proof of this in the oral and ventral enlargements which this spot shows on some segments, agreeing with the two chalazae, so distinctly developed in instar *V*.

The uppermost of the same row seems to me to be *m. dorsalis* and the double spot in the row caudal to the one I have just discussed, I consider to be *m. subdorsalis*, which is also double in instar *V*.

From this point of view the spot under it may obviously be considered as the large one under *m. subdorsalis* which has appeared in instar *V*.

The rows oral of the first-mentioned and caudal of the last-mentioned one agree entirely with those of the caterpillar.

We must still explain the spot, generally large, ventral of the stigma. In my opinion this is the *m. basalis*, which has nearly become irreconizable in instar *V*; and ventral of it a narrow, elongated spot agrees with the row of the *s. pedales*.

It is more difficult to explain the two spots between *m. dorsalis* and *m. suprastigmatis*. The more dorsal one of these two we may take as a part of *m. dorsalis*, which also in the larva often bears

two long setae, and with which indeed on the last abdominal segments of the chrysalis this spot becomes united.

The spot in between might correspond in this case to *chal. dorsolateralis*, which only occurs on the thoracic segments of the larva. If this is true, it would appear that this spot belongs to the abdominal segments as well as to the thoracic and has disappeared from them in a secondary way. If the last abdominal segments of the chrysalis did not show us pseudoprimitive conditions, this conception would become more probable. In the same way we might try to find the origin of the spot under *m. subdorsalis* in *s. subdorsalis inferior*.

Instar VII. *Imago*. J. F. VAN BEMMELEN could trace the same spots on the body of imagines which had not yet emerged. Here especially *m. infrastigmatis* and *m. poststigmatis* are distinct, the rows on the oral and caudal edges of the segments and the double *m. subdorsalis*.

#### Recapitulation.

1. It has been proved to be possible to reduce the intricate pattern of the last instar of caterpillars to the pattern, as it occurs in newly-hatched larvae.

2. This pattern of instar I agrees in the main with that of the caterpillars of other families. (Type I).

3. The pattern of the pupa and imago is more like this primitive pattern than that of the last instar of caterpillars.

4. In instar II the linea dorsalis, in instar III the linea stigmatis arises spontaneously i. e., without any stage of transition in the preceding instars.

#### *Pieris napi*. Linn. Plate V, fig. 8—13.

*Egg* laid apart on the lower and upper sides of cabbage-leaves and *Tropaeolum majus* L. It resembles that of *P. brassicae* but is  $1\frac{1}{4}$  mm. high and has 15 vertical ribs. Duration 6 days.

Instar I. Length  $2\frac{1}{2}$  mm. Duration 4 or 5 days.

The colour is transparent, bright-yellow with numerous copper-brown spots in vertical rows. The intestinal canal and the air-tubes shine through. Head provided with setae.

*Prothorax.* *S. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. dorso-lateralis*, *s. prostigmatis*, *s. basalis*, smaller *s. pedales*. No prothoracic shield.

*Mesothorax.* *S. dorsalis*, *s. suprastigmatis*, behind which a small *s. subdorsalis*, *s. prostigmatis*, *s. basalis*, smaller *s. pedales*. If a rudimentary stigma occurred, I certainly should have found it, as the tracheae were very distinct. The two lateral main-stems are connected with each other near the caudal edge of the segment (see Plate V, fig. 8 of instar I). Here the rudimentary stigma lies in the intersegmental membrane.

*Metathorax* = *mesothorax* but the above-mentioned *s. subdorsalis* is absent.

*Abdomen* 1, 2. *S. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. infrastigmatis* and *s. poststigmatis*, mostly small *s. basales*.

*Segm.* 3, 4, 5, 6 = 1, but the three *s. basales* are larger.

" 7, 8 = 1, but one *s. basalis*.

" 9. No *s. infrastigmatis*, one *s. basalis*, for the rest as 1.

" 10 = 1. No anal shield, but on the place which in *P. brassicae* agrees with this shield, three setae are found. Two *s. basales*.

" 11. Behind the three setae of 10, on the area of the anal shield of *P. brassicae*, three small setae arise agreeing with *s. dorsalis*, *s. subdorsalis* and *s. prostigmatis*. Ventral of these is a large one, which I consider to be *s. basalis*.

Instar II. Length 6 mm. Duration 4 days.

Between the primary setae we find many smaller ones and setae without a tuberculum arise on the leg. The primary ones remain distinct, they are much larger than the secondary ones, the setae are longer and thicker.

Of the secondary setae the vertical rows along the oral and caudal edges of the segment and many *s. basales* are conspicuous. Segment 11 is still clearly visible.

Instar III. Length 9 mm. Duration 3 days.

The whole body is now covered with numerous little knobs and setae between which the primary setae are clearly visible.

One seta situated over the stigma and *s. suprastigmatis* is quite like a primary tuberculum and therefore agrees with *s. dorsolateralis* on the thoracic segments. *S. infrastigmatis* has become double, but for the rest we hardly find under the stigmata any long setae with a well-developed tuberculum. There are many *s. basales*.

Instar IV. Length 13 mm. Duration 4 days.

The number of secondary tubercula increases, the primary ones e. g. on abd. segment 5: *s. dorsalis*, *s. subdorsalis*, *s. suprastigmatis*, *s. dorsolateralis* (arisen in instar III), *s. infrastigmatis* and *s. poststigmatis* remain distinct, the *s. basales* are indistinct. Under *s. subdorsalis* we find a new tuberculum which in form and size agrees with the primary ones and which therefore perhaps agrees with *s. subdorsalis inf.*

There is no real dorsal line, but exactly in the median plane the tubercula and setae are wanting, so that there the skin has a different aspect.

Instar V. Length 16—25 mm. Duration 8 days.

A dorsal line is faintly visible and coloured bright-yellow. In front of the stigma we find one yellow spot, behind it are two spots. There is no question of a stigmal line, but the prolongation of the spots is of a somewhat different colour to the rest of the skin.

The primary tubercula and setae are not distinctly visible, as many secondary ones resemble them very much. The pattern is lost and the animal makes the impression of possessing a coat of irregularly homogeneously spread setae. The tubercula are now coloured somewhat black. Under the stigma they are almost absent.

Instar VI. *Chrysalis*. Smaller than *P. brassicae* ( $\pm 20$  mm.).

I had at my disposal the variety which BUCKLER described (Vol. I, p. 158) i. e. the bright, tender green one with many spots.

The pupa quite agrees with that of *P. brassicae*, it shows dots corresponding with the tubercula of the larva mentioned below and the last segments are reduced in the same way:

*Macula dorsalis*, under it sometimes a small spot which in my opinion belongs to it.

*macula dorsolateralis*, sometimes double.

*m. suprastigmalis*.

*m. subdorsalis*, double.

*m. infrastigmalis* and *m. poststigmalis*.

two *m. basales* in one horizontal line.

one very tiny, elongated *m. pedalis*.

Here too we find an excellent correspondence between the spots of the pupa and the primary tubercula of the larva, which fact the more deserves our attention, as they had become totally irre- cognisable in the last larval instar. This is of great importance in connection with the conception of the colour pattern of the chrysalis.

#### Recapitulation:

I. The apparently homogeneous setae have been derived from the primitive pattern, as it occur in instar *I*.

II. This pattern almost completely resembles that of *P. brassicae* and other caterpillars. (Type I).

III. In instar *III* *s. dorsolateralis*, which at first only occurred on the thoracic segments, appears on the abdominal segments.

IV. The pattern of the pupa can be traced to that of instar *I*, not to that of instar *V*, but there is besides a spot in the position of *s. dorsolateralis*.

V. Linea dorsalis and stigmalis are indistinct, only in instar *V* they are represented by coloured lines and the last line is made up of spots near the stigma.

Family *Riodinidae*. As far as I know, no description of the larvae mentions a distinct setal pattern.

Family *Lybytheidae*. According to EDWARDS, quoted by FRACKER, the larvae resemble *Pieridae* as far as their setae are concerned.

Family *Nymphalidae*. This family is here taken in the same wide sense as W. MÜLLER did in 1886. Therefore the *Lymnadidae*, *Ithomiidae*, *Heliconidae*, *Agapetidae* are also included in it, together with the *Satyrinae*, *Danainae* and the *Nymphalinae* s. str.

GRUBER (1884) describes the development of the scoli from the primary setae, W. MÜLLER (1886) contradicts this. He says that

the scoli are formed from secondary setae, placed between the primary ones (c. f. Chapt. II and my Pl. I, fig. 1).

For this large group I refer to WEISMANN'S studies (1876) and to W. MÜLLER (1886). Where this family is concerned, FRACKER (1915) follows W. MÜLLER, but thinks that the expressions medio-dorsal, subdorsal etc. can be applied exclusively to "secondary" scoli and even then only when they are placed in one transverse row. This clashes with MÜLLER'S own ideas (l. c. p. 250).

The pattern of the primary setae is Type I on the abdomen, Type II on the thorax. I was only able to examine *Vanessa urticae* in instar I. This specimen already possesses scoli and secondary setae.

As I have cited in Chapt. II MÜLLER'S ideas on the *Nymphalidae*, I do not describe this caterpillar any further, but refer to Pl. V, fig. 14, 15, where instar I and abdominal segment 5 of the full-grown caterpillar are figured. I would rather draw attention to the pattern of the pupa which VAN BEMMELEN (1912) described. There is a small spine on the place of *sc. dorsalis*, and pigmental spots agreeing with *sc. dorsolateralis* (which is not developed on the abdomen of the caterpillar) *sc. suprastigmatis*, *sc. infrastigmatis*, *sc. basalis*, *sc. pedalis*.

#### Family *Papilionidae*.

In 1884 GRUBER described the larvae of the Swallowtail butterflies, instar I. To this paper too little attention has been paid by SCHULZE (1912), FRACKER (1915) and others.

GRUBER had a complete material of *Papilio asterias*, *P. turnus*, *P. troilus*, *P. ajax*, *P. philenor* at his disposal. All these caterpillars agree with each other in the fact that during instar I they possess verrucae with many setae, which in *P. ajax* are bifurcated, but in the others terminate in a knob. In *P. philenor* the tubercles bear only one seta.

During the ontogenesis these verrucae become smaller and at last are replaced by colour-spots, as can be distinctly seen in *P. asterias*. As far as I am able to see the arrangement on the

abdomen is: *v. dorsalis* small, *v. subdorsalis* large, *v. suprustigmalis*, *v. infrastigmalis* very large, *v. dorsalis*. The arrangement on the thorax is not distinct. *Verruca subdorsalis* maintains itself longer than the rest and this pattern reminds us of that of the *Lymantridae*.

W. MÜLLER (1886) is of opinion that the hairs of these *Papilionidae* may be considered as primary.

PIEPERS (1888) examined several Javanese *Papilionidae*. He says of *Papilio agamemnon* amongst others that in the beginning it has bifurcated hairs which have disappeared before the first moult. He thinks that they are bitten off by the caterpillars themselves.

CHAPMAN (1895, p. 88) says: "The young larva of *Papilio machaon* seems obviously reminescent of an adult *Vanessa*-larva. Yet it is certain that, whether *Vanessa* be or not be derived from a *Papilio*-like form, nor is there any probability that any adult *Papilio*-larva ever was spinous in precisely that manner. The spines are a special development of the young *Papilio*-larva for protective objects affecting itself. They have not been derived from spinous full-grown larvae amongst their ancestors, and are not passed on to the present adult larva, because it does not require them. The processus on the adult larva of *Ornithoptera* may be derived from the spines of the first stage and are not ancestral to those of the young *Machaon*."

FRACKER (1915) does not seem to know this. He only says on p. 138: "No unpleasant spines or horns are present to discourage the observer and no discordant colors to offend him."

SCHULZE (1912) discusses the *Osmateria* (Nackelgabel) and says they are derived from "dorsal protuberances". He points out the meaning of the ellipsoid glands as secretory organs, and thinks that they have no use in dispersing the *Ichneumonidae*.

*Sericinus telamon* Don., Coll. KALL., is covered with secondary setae which however are absent round many verrucae. Plate V, fig. 14.

The back part of the body has been a little damaged, so that I was not able to examine the anal segments. There are:

*Prothorax.* In the position of the *v. dorsales* the *osmateria*; *v. subdorsalis*, *v. prostigmalis* as a long spinule, *v. basalis*, *v. postpedalis* with only two setae.

*Mesothorax.* *V. dorsalis*, *v. subdorsalis*, *v. prostigmalis*, *v. basalis*, *v. postpedalis* with three setae and one verruca above the wing-rudiment.

*Metathorax* = *mesothorax* but the last mentioned verruca is only a pigmental spot, and such a spot is also found in the position of *v. infrastigmalis*.

*Abdomen* 1—9. *V. (sub?)dorsalis*, *v. infrastigmalis*, *v. basalis*, *v. pedalis*.

It seems to me that this form is very primitive.

I saw in some unpublished drawings of Prof. J. F. VAN BEMMELEN after specimens of *Papilio podalirius* from the collection KALLENBACH (which I could compare with the original objects) that the pigmental spots of the full-grown caterpillars are arranged in a definite pattern. In my opinion they agree with *v. dorsalis*, *v. suprastigmalis*, *v. subdorsalis sup.* and *inf.*, *v. prostigmalis*, *v. poststigmalis* and *v. infrastigmalis*. The presence of *v. subdorsalis inferior* and of *v. prostigmalis* is remarkable, as they do not occur in GRUBER's figures of instar I.

On the pupa of *Papilio machaon* (J. F. VAN BEMMELEN 1912, fig. 5) a tubercle stands in the position of *v. dorsalis*. Between the stigma and this tubercle there are two spots which therefore agree with *v. suprastigmalis* and *v. dorsolateralis*. So here too a *v. dorsolateralis* occurs on the pupa which is not developed on the abdomen of the caterpillars. Further there are spots on the pupa which agree with *v. prostigmalis*, *v. poststigmalis*, *v. basalis* and often *v. pedalis*.

As a larva, *P. machaon* varies very much in pattern. In most cases, however, the above mentioned spots are present.

## CHAPTER VII.

## COMPARISON BETWEEN THE PATTERNS OF CATERPILLARS AND THOSE OF THE PUPA, THE IMAGO AND OF OTHER LARVAE OF INSECTS.

From early days the pupae of butterflies have had a great attraction for the human mind.

The word *chrysalis* was already used by ARISTOTLE to indicate the goldecoloured pupae of some butterflies.

The conception of the pupal-stage has not always remained the same however. W. HARVEY for instance considered the pupa to be a perfect egg.

J. SWAMMERDAM who was the first to discover the wing-rudiment in the caterpillar, suspected that the pupa was not a new creation but that the result of another moult (1737, *Biblia Naturae* p. 567). He attached much value to the fact, that the setae of the caterpillars also occur on the pupa.

The majority of later investigators were convinced that the caterpillar is the primitive state and the pupa a secondary phenomenon. When the Darwinian ideas gained ground, it therefore became an important problem, how this resting stage had arisen.

The first who tried to give a solution was JOHN LUBBOCK (1871), in a paper which became very popular. He thought that the pupa was a form of transition between the larva and imago, necessitated by the great difference in the mouth parts. I think that the conditions of *Micropteryx* and *Eriocephala* definitely dispose of this theory.

LUBBOCK's opinion has been propagated by many treatises, but from the first another view has maintained itself against it.

BRAUER (1869) defended the opinion that it is the larva which has become modified and this conception has recently gained ground again.

RATZBURG's discovery of the external genital organs of the pupae (1840) was not paid attention to at the time, and thus it may be explained that JACKSON and POULTON thought they had described these organs for the first time (1890) after

having discovered them again respectively in 1875 and 1883. Though convinced that the larva is a phylogenetically old form, POULTON has still contributed much to propagate a new idea of the pupal stage. Many arguments are used by him to confirm his assertion that the pupa is a subimaginal stage, which has become immovable.

As his chief proofs I mention the well-developed external genital organs, the simpler structure of the wings, the large antennae and wings of those female forms, which in the imaginal state possess short ones, etc. The agreement in colour between caterpillar and pupa has been observed by him, but that feature he considered of little value.

J. F. VAN BEMMELN discovered in 1889, that the definite colour pattern of the imagines is preceded in the pupal state by a simpler one. More recent investigators confirmed this and BRYK (1914) demonstrated its persistence in an aberrative imaginal form.

PACKARD (1889) discovered that *Bombus*, before emerging from the pupa, moults once more, so that this reminds us somewhat of the subimaginal stage of the *Ephemeridae*.

In all these ways of considering the pupal instar it was taken for granted that all the Holometabola originated monophyletically. To this idea SWAMMERDAM has certainly contributed a great deal, and LUBBOCK too was of the same opinion.

BRAUER (1884, p. 318) directed attention to this problem without solving it, however. As it is closely connected with another question, namely: is it necessary that the setal pattern of the caterpillars agrees with that of the other larvae or can it be derived from it, I thought I had better give a short synopsis of the literature on this problem.

MIALL (1895) considers the incomplete metamorphosis of the *Orthoptera* to be a primitive one.

BOAS (1899) thinks the meaning of the pupal stage is to procure the animal the opportunity of developing its wings. His decisive assertion (p. 397) is incomprehensible to me: "Es ist demnach ausgeschlossen, dass das Insekt vor der letzten Häu-

tung seine Flügel entwickele". As he himself cites SWAMMERDAM's discovery of the subimago of the *Ephemeridae*, it must also be known to him that SWAMMERDAM described (*Biblia Naturae* I, p. 269 and *Historia Generalis* p. 87): "how in June 1670 in the neighbourhood of the village of Slooten, the subimagines flew upon his coat, that they moulted there and returned directly afterwards to the water." By this observation the argument of BOAS is refuted, in my opinion, more than two hundred years before it was used.

DE LAMEERE (1900) tries to find the origin of holometabolism in the habit, insects acquired by penetrating into vegetable tissues. The different Holometabola might therefore be derived monophyletically from the *Neuroptera*. HANDLIRSCH raises many important objections to these conceptions (See p. 126).

PÉREZ (1903) mentions several causes, but, as HENNEGUY (1904, p. 692) rightly observes, these are not explanations, but only statements of facts.

HEYMONS (1907) lays emphasis upon the great changes, which the so-called Ametabola undergo (e. g. *Machilis*). He says on p. 160, that the pupa is a new stage. Naturally we must not think that no trace of it is to be found in the lower insects: „Es kann erstens die Holometabolenpuppe das umgewandelte letzte Larvenstadium oder die Summe der letzten Larvenstadien der Hemimetabolen repräsentieren, oder es kann zweitens die Puppe weiter nichts als eine unvollkommene Imago selbst, gewissermassen eine vorläufige noch unfertige Ausgabe der Imago sein." HEYMONS adopts the latter alternative and is therefore an adherent of the subimaginal theory. He thinks besides that the Lepidopterous pupa has become secondarily movable again. In this connection I think attention should be drawn to the investigations of CHAPMAN (1893) who demonstrated that it is exactly the *pupa incompleta* which occurs in the lower families. He also directed attention to the fact that the pupae are generally much more movable than is usually supposed. In my opinion the movability of the Lepidopterous pupa is to be considered a primitive characteristic.

DEGENER (1909) supposes the rigidity of the chitinous skin to be the cause of the moultings and he thinks (p. 19 sqq.): "that the higher specialized insects possess a tendency and a will to diminish the number of these moultings. This can only be achieved by retarding the development between two moultings, and so attaining by one ecdysis what otherwise could only be attained by many. The more these moultings were reduced in number, the less recapitulations of phylogenetic stages had to be passed by the larva, and so it makes the impression that phylogenetically its development is retarded, and ontogenetically it remains all the longer in a primitive state, by retardation of its development. Through this, the larva has the opportunity of specializing itself, according its own desire and character. The great difference has arisen in consequence of a different manner of life, especially the aquatic one. Pupa and subimago are not identical, but they are both primary stages of development, which have remained preserved."

BASTIN (1913) and CARPENTER (1913) are both adherents of the subimaginal theory, especially the latter, who has published a short but very interesting treatise, which contains a great many facts and is written with great conviction.

In constructing a theory on the origin of the pupal state it is necessary to study the subject from as many different points of view as possible. By WEISMANN'S investigations especially (1863, '64, '66), later on continued by i.a. J. VAN REES (1888), MESNIL and METSCHNIKOFF (1900), BAUER (1904), JANET (1909) and POYARKOFF (1910), the attention of the investigators has been turned more to the histological processes and in the first place to the histolysis in the pupal stage, than to the purely morphological problems. Histolysis may be considered to be a secondary phenomenon, but from that it does not follow that the pupa itself is secondary. The larva of a frog is not secondary because its tail disappears by phagocytosis! It is therefore desirable to direct the attention to palaeontology, which has been greatly neglected by many entomologists. On this point I refer especially to the last of the three following writers:

SCUDDER (1886), BRONGNIART (1894) and HANDLIRSCH (1903, '06, '10). ZITTEL-BROILI (1915) agrees with the latter in the main points.

The number of fossil insects has now become so considerable, that the existence of a palaeo-entomology can no longer be denied. The principal lines of the genealogical tree can already be drawn.

HANDLIRSCH (1903, p. 720 sqq.) directs attention to the fact, that originally the abdomen consists of 11 segments and a telson, the 11th segment bearing a pair of cerci.

In the Palaeozoic era there are only Ametabola; all the different Metabola appear at about the same time, namely in the Permian formation.

In the Palaeozoicum the relatives of the Polynephria are found, in Perm and Trias the Oligonephria appear. From the fact of their synchronistic appearance it follows, that perhaps a polyphyletic origin of the higher orders may be assumed, which orders therefore appeared as parallel lines. In the Perm the branch of the *Neuropteroidea* and that of the *Coleopteroidea* are already separated from that of the *Panorpoidea*. To the latter belong the *Phryganoidea*, *Panorpatata*, *Lepidoptera*, *Suctoria* and *Diptera*. This classification differs entirely from that of LAMEERE.

HANDLIRSCH adduces against this writer (1900, p. 174):

1°. The reduction of the cross-veins. Very often the recent holometabolic *Neuroptera* and *Sialidae* still show a more original vein-course than the carbonic *Megasecoptera* (the primitive group of the *Panorpoidea*), besides the reduction of the veins is a common feature in Heterometabola.

2°. The habit of carrying the wings in a horizontal position is only found in Heterometabola, these alone have well-developed cerci; the *Megasecopteros*-larvae also had wing-sheaths like that, and therefore were probably heterometabolic too.

3°. The *Lepidoptera* are originally phytophagous and they only become secondarily endophagous. In this case organisms would have been driven in a progressive direction by the influence of parasitism according to LAMEERE, whereas as a rule they degenerate by it.

4°. If we adhere to a monophyletic origin of all Holometabola,

the holometabolic *Palaeodictyoptera* must have been the ancestors, but then the Heterometabola must have been developed polyphyletically, and what was always considered as being primitive, would turn out to be secondary.

None of the different causes of holometaboly, given by the other writers which I have already quoted, can be the reason according to HANDLIRSCH, because many larvae have remained phytophagous, and nevertheless are still heterometabolic. Neither can endophagism be the reason, because nearly all the Holometabola are carnivorous or phytophagous. Heterometabola as well as Holometabola can lead an aquatic or subterraneous life, so that only meteorological causes remain. The beginning of many groups of the Holometabola at the same geological period, namely in the transitory period between Palaeozoicum and Mesozoicum, also indicates a heterophyletical origin. Perhaps the glacial age of the Perm has been the decisive factor. However this may be, it is certain, that HANDLIRSCH, on account of his extraordinary knowledge of fossil insects, does not think that the monophyletic origin of all Holometabola is possible. For the problem which I am endeavouring to solve, this means that the skinreliefs of the larvae and nymphae of the different orders need not necessarily agree with each other. I will soon refer to this point again, after having compared the pupa of the Lepidoptera with the caterpillar.

POULTON (1890, p. 193) drew attention to the fact that the pupae of the *Sphingidae* exhibit for a short time the same pattern which the caterpillars possess in the last instar. The stripes, however, are secondarily hidden by a brown colour, in regard to which it should be noticed that the wings and other new-formed parts adopt this colour later than the organs already present in the larva. POULTON did not attach much value to these stripes, for he says: "The persistence of such colours depends upon the fact, that the hypodermis-cells of larva and pupa are the same, so that any pigment contained in them during larval life, may remain unchanged after the pupal period has begun".

Though I have great confidence in POULTON's knowledge of

morphology, yet I think I am allowed to oppose LAMEERE's opinion (1900, p. 623) to his, viz. that the hypodermis is entirely renewed by histolysis. Besides the colour-pattern of the pupae cannot be a simple copy of the larval pattern.

J. F. VAN BEMMELEN (1912, p. 111—117), has observed that the hypodermic pigment has also a morphological importance and he succeeded in demonstrating, that the same pattern exists on the pupae of *Pieris brassicae*, *Aporia crataegi* and *Euchloe cardamines*, and that this pattern agrees to a great extent with that of *Papilio machaon* and *Vanessa urticae* and *V. io*. The caterpillars of these butterflies differ a great deal in their pattern. VAN BEMMELEN thought, that a great resemblance was to be remarked between the pupal markings and the larval pattern of *Pieris brassicae*. He took this to be the colour-pattern of the once movable chrysalis.

On this idea I have based my investigations. In the main I agree with VAN BEMMELEN's opinions, with this restriction however, that I should not compare the pattern of the pupae with that of a full-grown caterpillar of *Pieris brassicae*, but with the pattern of instar I.

In chapter VI I have shown that the colour-pattern of *Pieris brassicae* and that of *P. napi* instar I, closely resemble that of the pupa. Compared with the last larval instar of the first species a reduction of the number of pigment spots has taken place, with that of the last mentioned on the contrary, a strong accrescence of the number.

This is a convincing proof of the inexactness of the statement that the pupal pattern should be a simple copy of existing hypodermal pigment.

J. F. VAN BEMMELEN demonstrated the same pattern on the pupae of different *Pieridae*, *Papilionidae* and *Vanessa* spec. In this article I have given further details for many families. The arrangement of the verrucae on the pupae of *Ocneria dispar* and *Orgyia antiqua* is also the same. SWAMMERDAM already indicated this last fact (*Biblia Naturae*, 1737) and POULTON (1890, p. 193) also called attention to it.

QUAIL described (1900, p. 416, Pl. V) the pupae of *Porina cervinata* Walk. (*Hepialidae*) and showed here the same setal

pattern as on the caterpillar. The pupae of *Hepialus lupulinus* in the coll. KALL are a little damaged, yet they show setae arranged, in my opinion, as in type I, augmented by *s. dorsolateralis*.

It seems to me, that these are remnants of a formerly common pupal pattern, consisting of setae which had accumulations of pigment at their bases. Just as is the case with the caterpillars, the pigment spots can remain after the disappearance of the setae. I cannot but think that this pattern of the pupae has taken origin on a movable animal. Therefore I believe that I am allowed to consider these remains of a pupal pattern as a proof of the theory, that the pupa is a subimaginal stage which has secondarily become immovable. Consequently the pupa is not a phylogenetically younger form, but a preserved primitive form which has become secondarily immovable. The agreement between the pattern of the caterpillar instar I and the pupa is so striking, and the differences between the pattern of the last larval instar and the pupa are often so considerable, that it becomes interesting to try to solve this problem.

I believe that this can only be explained by accepting the first larval instar as well as the pupa as primitive forms, but the following instars as newly acquired ones. The latter instars are all specialized in different ways. DEGENER (1909) has also advocated this hypothesis. Some instars become bearers of warning colours, others obtain long thick tussocks, a third group retains the primitive type pretty well, because it lives in hidden places, but, when the pupal stage has begun, the old pattern returns, to be sometimes overspread by a homogeneous colour.

Even on the imagines (J. F. VAN BEMMELEN, 1912) the old pattern is sometimes to be seen. W. MÜLLER (1886) thought that the pattern could pass from the caterpillar on to the pupa, and also the other way about. I think I have proved by the detailed account of the *Pierids*, that in this case it certainly cannot be true. Therefore we must return to the opinion of WEISMANN (1876), who concluded from all these phenomena: "dass die Errungenschaften der einzelnen Stadien in den folgenden Gene-

rationen immer nur auf diese Stadien selbst wieder übertragen werden, die andern Stadien aber unbehelligt davon bleiben" (see p. 6 sqq. chapter II).

If the first larval instar as well as the pupa both show primitive conditions, it may be that the colour pattern borne by both, is so old that it also appears in other orders of insects. In that case it has already been obtained before the separation of the different orders, i. e. in the under-carbonic period. Considering that the families of *Lepidoptera* were separated, according to HANDLIRSCH (1906), in the cretaceous period, and hence the genera and species still later, no great result can be a priori expected from such an investigation. In the following I intend to discuss the orders, which are in some way related, although I think that such a discussion has only a very relative value, if it is not supported by a very extensive investigation. But for that I lacked time and material.

HANDLIRSCH thinks that the *Panorpata* are in some respects to be considered as the ancestral form of the *Lepidoptera*. It is certainly of great value, that J. BOTKE (1916) came to the same conclusion through his investigation of the colour-pattern of the *Lepidoptera*, differing in this from DE MELJERE (1916).

Having explained in chapter VI that in different families, independently of each other, verrucae have appeared, and directed attention to the fact that sometimes within the precincts of one family rather important differences in the setal pattern occur (c. g. *Hepialidae*, *Pterophoridae*, *Pieridae*), it is not to be expected that other orders should show the same pattern.

The existing illustrations of the larvae of the *Panorpatae*, *Neuropteridae*, etc. are still less exact than those of the Lepidopterous larvae. Besides I think that in the preceding lines I have sufficiently pointed out, how only complete series can give us a good idea of the real character of the setal pattern and that conclusions, reached by comparing the full-grown forms only, can easily lead to wrong hypotheses. It is therefore with the greatest reserve that I submit the following remarks on the setal pattern of insect-larvae.

BRAUER devoted some articles to the larvae of *Panorpa communis* (1851, 1852, 1863). He found that the larvae bear setae in instar I, later on verrucae. According to the figures, on all the segments three setae occur arranged in a row above the stigma. The arrangement of the verrucae cannot be clearly seen in his figures. It is certain that *verrucae* occur (braune hornige Warzen) with rather short setae.

FELT (1895) described the *Scorpionflies*, but in his work the setal pattern is not very distinctly indicated either. In connection with the fact that there are verrucae on the *Eriocephalidous* larvae and also on numerous other families, one would almost be inclined to consider the verrucae as being primary. The simple setae of the higher families might in that case be taken to be a secondary characteristic. The disappearance of the verrucae on the *Papilionidae*, the *Bombycidae*, the *Endromidae* and the *Brahmaeidae* could then be used as an argument in this direction. However, it seems to me that this hypothesis should not be accepted. As far as I can judge, the verrucae in all the families are formed from simple setae. The verrucae of the *Eriocephalidae* differ too much to be a strong proof of the hypothesis and they take origin from single setae; the disappearance of the warts in the three above-mentioned families of the SYMBOMBICIDAE is easily explained as a reduction of the verrucae by the development of a homogeneous setal cover. It is the same with the *Acronyctinae* and the *Papilionidae*. In spite of CHAPMAN'S statement (1902) I consider the verrucae of the first instar to be rudiments of scoli which formerly were more strongly developed. DYAR (1894) thought that the setal pattern of the *Tenthredinidae* was the ancestral pattern of the *Lepidoptera*. This writer adheres to the monophyletic origin of all the Holometabola. There are nine setae on either side of an abdominal segment and they are placed in three rows each containing three, of which the middle one is right over the stigma. He supposes, that in *Lepidoptera* the first of these rows has disappeared, except perhaps *s. prostigmalis*; the second row should agree with *s. dorsalis*, *s. dorsolateralis* and

*s. suprastigmatis*. *S. subdorsalis sup.* and *inf.*, as well as *s. poststigmatis* might perhaps be derived from the last row. Such an explanation seems to me a little farfetched; besides the anatomical differences between the *Hymenoptera* and the *Lepidoptera* are too great to accept such a near relationship between these orders. Neither do the palaeontological data harmonize with DYAR's opinion.

At present several writers defend a nearer relationship of the *Lepidoptera* with the *Neuroptera*, amongst others CHAPMAN (1896) and DE MEYERE (1916). With HANDLIRSCH, I believe that the palaeontological data do not agree with this hypothesis. I could not get any proper data about the larvae of the *Neuroptera*. According to the figures in the manuals the larvae have very different forms; some are naked, others are covered with long setae. The arrangement also seems to be very different (OUDEMANS 1897, p. 317—323).

The figures of the *Trichoptera*, the caddicee worms, are much better. SILTALA (1907) studied them accurately. In this order also there appears a secondary augmentation of the setae during the ontogenesis. In the first instar the setae of the larvae are only very sparse. He could not find an agreement with the setal pattern of the *Lepidoptera* and by studying his figures I came to the same conclusion. The pupae are sometimes also covered with setae and some larvae (e. g. *Hydropsyche*) bear verrucae, though mostly simple setae.

As the *Trichopterous* larvae have certainly undergone profound secondary modifications, I think that too much value must not be attached to the arrangement and form of their setae, though they belong to the *Panorpoidea* and though CHAPMAN (1896 c) associates the *Phryganeidae* and the *Micropterygidae* together.

Although I do not believe that the *Coleoptera* and the *Lepidoptera* are closely related, I still think it necessary for the sake of completeness to compare the setal pattern of *Leptinotarsa* with that of the *Lepidoptera*.

The classical investigations by TOWER (1906) have drawn great

attention to this genus, and from his very accurate figures it is easy to study the pattern. TOWER distinguishes two rows of spots on the abdominal segments, the anterior and posterior band of tergal spots, each consisting of three spots, placed in a vertical row, namely the inner, middle, and outer tergals. Behind them comes the spiracular spot and then the basopleural one. Ventral of these are placed two rows each consisting of three spots, the outer, middle and inner sternal spots.

On the mesothorax and metathorax these spots are partly united, and in the position of the spiracular spot there is a wing-spot. The prothorax differs a great deal and possesses a prothoracic shield, with an anterior and a posterior pronotal band.

I think it an important fact that in these *Coleoptera* two rows of three spots occur above the stigma. The *Tenthredinidae*, which are certainly not so closely related, have three rows, each consisting of three setae; on the *Panorpata* one row of three is found and on the *Lepidoptera* I think that the row above the stigma also consists of three, including the *s. dorsolateralis*.

In this connection the spot on the pupae agreeing with the *seta dorsolateralis* acquires a greater importance.

It seems to me that these three spots or setae, placed in a vertical row, have been acquired in very remote periods and that the meso- and metathorax, though they have suffered profound secondary modifications, have best preserved them.

DE MEIJERE (1916) recently published an interesting study on the wing-markings of *Diptera* and *Lepidoptera*. He has also made a study of the larval pattern. His paper reached me too late to consider it in dealing with the different species, and therefore I may quote his main result here.

On p. 63, the author says, that it seems to him as if, when a depositing of pigment has become physiologically necessary, it is indifferent where that process takes place. It is only restricted to the sixteen places or patterns given by him. I cannot agree with this in so far as the larval and pupal body are concerned.

When he says p. 64 that in one and the same family the

patterns belong to different evolutionary rows, I can refer to pg. 137 and 139 where I have stated the same opinion. The pattern itself comes back in different families (l. c. p. 75) and DE MEIJERE is of opinion that this has been caused by parallel evolution, whereas I am convinced that generally spread patterns are phylogenetically old ones.

On p. 132—133 DE MEIJERE discusses the colour pattern of the abdomen of *Lepidopterous* imagines. He agrees with J. F. VAN BEMMELEN in considering the spotted ones as primitive.

DE MEIJERE (l. c. p. 136—143) compares the larval pattern with the pupal one. He states the fact that the colour first appears at the bases of the sensory setae (Sinnesborsten) e. g. on *Diloba*, *Zeuzera*, *Hydroecia*, *Pieris* instar I, *Abraxas*. The last mentioned species is highly interesting as SCHRÖDER (1894) says that the stripes appear first. (see p. 20)

So far I agree with DE MEIJERE. This writer however rejects the hypothesis of the primary pattern of *Lepidopterous* pupae, and his chief argument is that the *Neuroptera* are the common ancestors, from which the *Trichoptera*, *Panorpata*, *Diptera* and *Lepidoptera* were differentiated, after having acquired the holometabolism. All these primitive forms and also the lower *Lepidoptera*, as e. g. *Micropteryx*, have but slightly coloured pupae, which live hidden in the earth or in cocoons.

I refer in the first place to HANDLIRSCH and in the second instance I think that in the foregoing pages I have given several proofs of my thesis, that the pattern of pigment spots is the same as the setal pattern. This setal pattern however is widely spread amongst the uncoloured pupae, and so I suppose that this setal pattern (type I) is an old phylogenetical one, and that the pigment spots, in larvae as well as in pupae, follow this arrangement. The pupae of the *Rhopalocera* are secondary in so far as they have lost the setae, but have only retained the pigment spots. The pupae which have become immovable and therefore often remain in the earth or in a cocoon, have secondarily lost the pigment, but have often preserved the setae.

## CHAPTER VIII.

## GENERAL CONSIDERATIONS AND SYNOPSIS OF THE RESULTS.

In the preceding pages I have tried to lay down a general foundation for the armature of caterpillars.

In consequence of the shifting of the stigmata over mesóthorax and metathorax and the development of the wings on them, I take it for granted, that these segments are to be considered as being secondarily modified.

On account of the anatomical differences with the abdomen, this result might a priori be expected, and the chaetotaxy on these segments provides proofs that the setal pattern also has undergone secondary modifications. The prothorax too has taken part in these changes by obtaining the stigma which originally was placed on the mesothorax. Hence it is not desirable to start from these segments in reconstructing the primitive pattern, as TSOU and FRACKER have done (Chapters III and V).

The anal segments too differ in structure and even vary in number. This probably happens in connection with a process of reduction which in some species has farther advanced than in others (Chapter IV).

Among the remaining eight or nine abdominal segments a few occur bearing legs and others without them. On account of embryological facts as well as of the presence of the *setae pedales*, I think it allowable to consider the segments with legs as the more primitive ones (Chapter IV).

From the literature, Chapter II, it appears that all the different investigators of the setal pattern have introduced a nomenclature of their own, in which many made use of numbers. As some of them indicated totally different setae by the same number and as the same setae are indicated by different investigators by widely different numbers, a great confusion has arisen, as is best illustrated by Plate I, fig. 1—21.

I have therefore been led to use a nomenclature which agrees with that of WEISMANN, W. MÜLLER, SCUDDER and J. F. VAN BEMMELEN.

The setae on an abdominal segment are indicated by names which refer to the place of the implantation.

An identical system has been applied to the thorax in which the same names as far as possible are used.

Where the homology with the abdomen is not very clear, the changes in the position of the setae have been indicated by other names, because I think that a nomenclature should be a means of describing a thing in a short and clear way, and not an expression of more or less probable hypotheses.

The shortest method of description certainly is to indicate the whole of the setae on a certain segment as Type I.

The other ways of arrangement on the abdomen, Type Ia and Ib, can be derived from Type I, by assuming reduction.

The thoracic segments differ most of all and are called Type II. Very often a reduction of the number of setae has taken place on their dorsal side, but at their oral border there is one seta more than usually occurs on the abdomen. This seta I have called *s. dorsolateralis* and in so doing I disagree with other writers. By especially studying the setae and the pigmental spots on the pupa and by an accurate comparison of the prothorax with the abdomen, I have come to the conclusion that this seta does not correspond to *s. subdorsalis* as is generally accepted.

On the mesothorax and metathorax a pigmental spot is often to be found in the place where we might expect the stigma, if this were exactly situated as on the prothorax. Most investigators have taken this spot to be the rudimentary stigma. It is by studying BOAS, that I have come to the conviction that this is not the case, but that this spot agrees with the wing-rudiment.

A shifting of the stigmata must have taken place and by means of this fact I have tried to explain Type II (Chapter IV). Like QUAIL I consider the seta in front of the wing-rudiment to be *s. prostigmalis* (III B.).

For their bearers the setae may be useful in several ways, but it is difficult to assume, that any correlation could possibly exist between usefulness and arrangement of pattern. The consequence

is, that we may expect changes in the pattern to possess a certain systematical value. Though this rule is not always adhered to, it generally holds good.

Of the setal pattern of caterpillars we may say what CHAPMAN says of the pupa: "The Lepidoptera certainly cannot be arranged in one line by their pupae, but the Lepidoptera of one line can be arranged by their pupae." In studying the pattern we get the impression of many lines of development which often run parallel. This completely harmonizes with HANDLIRSCH's opinion and with that of DE MEJERE.

Before passing on to the discussion of the families, I wish to devote a few words to the biological signification of the setae, FRACKER assumes (1915, p. 38) that the setae are sensory in function.

QUAIL (1900) thinks that the setae of the *Hepialidae* can open and shut, WACHTL and KORNAUTH say that the special setae of *Psilura* serve to facilitate the spreading of the caterpillars by the wind. Usually it is thought, however, that the setae serve as a means of defence against enemies, especially *Ichneumonidae* and *Tachinidae*. This opinion has particularly been propagated by PACKARD and POULTON. I think I may call it into doubt. The experiments of the last-mentioned writer give us a right to assume that a dense covering of setae or tufts and long pencils, form a means of defence against some vertebrates, but the results he obtained cannot be directly transferred to enemies of the insect-tribe. In structure the eyes of the insects differ so much from those of the vertebrates and are so absolutely different in their sensibility to colours, that we may not treat the problems which here present themselves, from a point of view so anthropomorphic, as for instance POULTON does, in his well-known and interesting book: *Colours of animals*. On page 87 he says: "A person unaccustomed to the observation of the animals (the light-coloured trout) would certainly fail to detect any trout except the black ones, which were blind and did not vary their colour". I must confess that I fail to see the value of this argument, as I am

convinced that the enemies of the trouts are certainly accustomed to observe and detect them.

The results of my experiments in cultivating *Acronyeta psi* and *Pieris napi* — only to mention two widely differing forms — brought me to the same conclusion as W. MÜLLER came to, after an experience of many years viz: that naked forms are as much afflicted by *Ichneumonids* as the species which bear large spines.

In the first instar many setae are so-called glandular hairs.

The systematic signification of these generally bifurcated setae cannot possibly be very great in my opinion. They occur in numerous families: *Papilionidae* (GRUBER, 1884), *Nymphalidae* (W. MÜLLER, 1886), *Notodontidae* and *Pterophoridae* (PACKARD, 1890), *Pieridae* (SHARP, 1901) and *Sphingidae* (PACKARD, 1905). For this last family I have given an accurate description of the form and it was only later on that I studied PACKARD's drawing which differs in some respects from mine.

Also outside the order of the *Lepidoptera* we may find these setae, i. a. on *Periclista melanocephala* F. (*Tenthredinidae*). Like the setae of *Psilura*, described by WACHTL and KORNAUTH, which I found again in *Ocneria* and the peculiar elevations of *Heterocampa* (PACKARD, 1895), I consider them to be rudimentary organs which are disappearing and which now do not possess any important function for the welfare of their bearers.

I should not be astonished if it were found that the monosetal tubercula originally have been tactile organs.

In numerous families the monosetal tubercula developed into warts (verrucae), without it being possible to attribute any systematical importance to this feature.

In my opinion more importance should be attached to the setae being plumose or not. As far as I know plumed setae only occur on those caterpillars which possess verrucae, but not even on all of them. The only exception known to me is the family of the *Hesperidae* of which FRACKER says on p. 127 "The head is covered with numerous secondary setae, often plumose but never long, sometimes borne on chalazae."

This case excepted, it seems to me that we can prove that the feature of plumose setae has been obtained later than that of verrucae.

If this observation should also be confirmed for other species than those I had at my disposal or for those of which I was able to collect data from the literature, this might add to a more accurate insight into the phylogeny of the *Lepidoptera*.

SCUDDER's opinion that a homogeneous spreading of the setae over the segment is a primitive quality, is decidedly wrong. Naked forms and species with a dense covering of setae have always arisen from species with a definite setal pattern. (Chapter VI i. a. *Bombyx*, *Sphinx*, *Pieris napi*).

The verrucae of some families are reduced again to setae. Now in palaeontology the law of irreversibility holds, which DOLLO (1893) formulates in the following few words: "The development goes on with leaps, is irreversible and limited."

In discussing the families I have drawn attention to the fact that it can sometimes be seen from the whole pattern, but often not from the separate setae, whether they have arisen primitively or by reduction of the verrucae.

In any case therefore for the separate organs we have to do with a reversible development, a fact which deserves our attention in connection with the interest which from the palaeontological side especially is paid to this problem [compare for instance the exceedingly clever expositions by DÉPÉRET (1908) and by his critic HOERNES (1911)].

The objections which FRACKER (1915) makes to my opinion explained above, do not appear to me to be quite convincing. For particulars I refer to the *Noctuidae*, Chapter VI.

Concerning the separate series of development I can sum up my results in the following way (Chapter VI):

The *Hepialidae* differ rather from the FRENATAE, but at the same time present such important differences from the other JUGATAE and even amongst themselves, that it is impossible to fix a definite, strictly circumscribed pattern for this sub-order. Verrucae occur on the *Eriocephalidae*.

There is very often a *s. dorsolateralis* on the abdomen.

Of the so-called MICRO's the PYRALOIDEA differ from the others by a slightly altered arrangement of the setae and by the formation of verrucae.

The BOMBYCES seem to be descended from forms with monosetal tubercula which are developed into verrucae. In the more specialized families these verrucae disappear and they are only distinct during instar *I*. A reduction of the number of setae is often to be found.

The *Noctuidae* too originally possess monosetal tubercula which are transformed into verrucae and afterwards are again reduced to simple setae.

The *Sphingidae* i. a. differ by the presence of a *s. prostigmalis* and the absence of *s. poststigmalis* on the abdomen.

The RHOPALOCERA in so far agree with each other that the primitive setal pattern becomes supplanted during the ontogenesis by another arrangement of the setae. On the pupa, however, type **I** appears again. The presence of verrucae during instar *I* of the *Papilionidae* can be explained as a last remnant of the dermal armature they formerly possessed.

A comparison with the rest of the orders of insects did not yield many results. I could find however an indication of a general groundform which consisted in an arrangement of the setae in rows of each three on either side (Chapter VII).

I have the impression, that it is under EIMER's (1874, 1889) influence that WEISMANN (1876) came to attach such a particular value to the stripes. Later on ESCHERICH (1892) and SCHRÖDER (1894) advocated the same hypothesis. In opposition to it J. F. VAN BEMMELEN (1889 sqq.) tried to introduce his opinion, that not stripes but spots compose the primary pattern. J. BOTKE (1916) in his studies comes to conclusions which in the main agree with this opinion. DE MEIJERE (1916) comes to the same conclusion. J. H. KRUIJEL also rejects EIMER's hypothesis, after his study of the feathers of the Gallinae (1916). TOWER (1906, p. 226) says "in ontogeny and in evolution (species foundation)

color appears first in centres which upon the body are metamericly repeated spots."

These writers, however, belong to the few who do not consider the stripes to be the most primitive element of the pattern.

From my investigation it appears to me that the pigment first accumulates round the bases of the setae or in the verrucae, so that the primary pattern consists of pigmental spots arranged according to type I. This pattern is repeated on each segment and hence has a metamerial character.

The stripes arise in the ontogeny either simultaneously with or later than these spots and are therefore a new characteristic.

I have tried to find a form in which I could trace the development of a stripe and I think I have succeeded in *Phalera bucephala* (see p. 65 sqq.). In instar I the ordinary pattern (type I) is present. In the course of the development the number of spots increases a great deal whilst the original pattern gets less distinct. The secondary spots are situated in vertical rows but by a consolidation of some primary and secondary spots a horizontal stripe arises. This stripe, however, is less sharply confined than is usually the case on caterpillars, so that I am not quite sure whether all the stripes are developed in the same way. It may also be that the stripes have suddenly arisen, perhaps as mutations.

It is however a fact, that the pigment spots arranged like type I, form a phylogenetic element of the pattern which is older than a stripe.

Under EIMER's influence we have entirely forgotten that a stripe, i. e. an alteration of a certain part of a segment over the whole breadth, is altogether a different thing from the series of spots arranged on the segment in a certain pattern.

A group of spots like this, will be repeated on all the segments, because of the strong homoiomery which governs the structure of the body of caterpillars, but a continuous stripe is quite an other thing, for it is an alteration of a certain part of the skin over the total breadth of the segment.

Such an alteration does not happen on the other organs either.

It quite agrees with this that a stripe appears later than a certain pattern of the spots. In the descriptions of the *Pieridae* and *Phalera* amongst others, proofs have been given of the fact that EIMER's hypothesis does not deserve adherence and that J. F. VAN BEMMELEN and TOWER are right in defending their opinion that a pattern of spots is more primitive than a stripe. The agreement of the pupal pattern with that of the caterpillar instar *I* was proved to be so great, that an accidental agreement is out of the question. The differences of the pupal pattern with that of the last larval instar are often so great that there is no possibility of the pupal pattern resulting from the remaining parts of the larval hypodermic pigment.

On these facts I have based the theory developed in Chapter VII, that the pattern of the larval instar *I* as well as those of the pupa and imago are primitive characteristics.

The differing armatures of the other larval instars have arisen from specialisation in connection with the mode of life of the caterpillars.

The later larval instars have arisen from a retardation of the development and with it the setal pattern has had the opportunity of differentiating in various directions. From this we see that I arrive at the same conception of the larval instars as DEGENER did on the ground of totally different investigations.

Summarizing my results, I come to the following conclusions:

1. The organisation of the thorax is secondary.
2. The anal segments change in number in the various species of larvae.
3. Originally all abdominal segments were provided with a pair of legs.
4. In connection with earlier writers a new nomenclature has been given for the arrangement of the setae: type I, *Ia*, *Ib* and II.
5. These various types can be derived from each other.
6. A metamericly repeated pattern of pigment spots is more primitive than a pattern of stripes.
7. The change of setae into verrucae is a reversible process.

8. From the agreement of the pupal pattern with instar *I* and the difference with the last larval instar, the hypothesis has been developed, that the pupa and the first caterpillar instar are both primitive states.

9. The other larval instars are to be considered as secondary adaptations.

10. The pupa is to be considered as a subimaginal stage which secondarily has become immovable.

11. The various caterpillar families have for the greater part developed themselves independently of or parallel to each other.

12. A general larval pattern for the Holometabola is as yet not to be established with certainty.

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## EXPLANATION OF THE PLATES.

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### PLATE I. Synopsis of Nomenclature, 1886—1916.

- Fig. 1. *Mysectia orsis* (*Nymphalidae*). Instar I. Immediately before moulting. To show the arrangements of the primary setae and the place of the secondary scoli. After W. MÜLLER (1886, Taf. 3, fig. 14).
- » 2 and 3. *Acræa pellenca*. Hübn. (*Nymphalidae*). Instar I. To show the primary setae on the metathorax and the 2nd and 3rd abdominal segments, after W. MÜLLER (1886, Taf. 1, fig. 1).
  - » 4. *Hepiatus lupulinus*, after H. G. DYAR (1894, p. 197). Observe the three setae above the stigma.
  - » 5. The arrangement of verrucae is of the "Arctian type", marked according to H. G. DYAR's system (1894, p. 198).
  - » 6. An abdominal segment of a *Psychid* larva. Adapted from a figure by H. G. DYAR (1884, p. 198). Observe the three setae above the stigma.
  - » 7. Thoracic scheme, marked according to DYAR's system (1894 b).
  - » 8. Thoracic scheme after O. HOFMANN (1898). The subprimary setae are marked with an asterisk. H. G. DYAR himself agreed with this system in 1901. The differences between his opinion at this date and that of 1894 are given in Roman cyphers.
  - » 9 and 10. *Melanchria nutans*. (*Noctuidae*). Instar II. The setae on a metathoracic and an abdominal segment, after the ideas of A. QUAIL (1904 b). Mark seta III B.
  - » 11 and 12. Metathorax and abdomen with primary setae, according to the system of W. T. M. FORBES (1910), cited by ST. B. FRACKER (1915).
  - » 13. *Pieris brassicae* L. Instar V. The rows of pigment-spots, with the names given by J. F. VAN BEMMELEN (1913, p. 115).
  - » 14. *Hepiatus humuli*. Metathorax and 1st abdominal segment of a mature larva. Adapted from a figure by Y. H. TSOU (1914, Pl. X, fig. 1 c, d). Compare figure 4, 22, 23, 24, 25 of this plate.
  - » 15. Hypothetical type showing twelve primary setae. The three usual subprimaries are dotted in. The spiracle is shown in both prothoracic (thor.) and abdominal (abd.) positions. After ST. B. FRACKER (1915, Pl. I, fig. 1).

- Fig. 16. *Atteva aurea* (*Yponomeutidae*). Metathorax. To show the thoracic setae of a typical *Micro*. After ST. B. FRACKER (1915, Pl. V, fig. 36).
- » 17. *Feltia glandaria* (*Noctuidae*). Instar I. 6th abdominal segment. Marked according to ST. B. FRACKER'S system (1915, Pl. IV, fig. 29). Note seta  $\rho$  in this figure and in figure 15.
- » 18. Mesothoracic and metathoracic scheme, according to my view. Type II. Note the wing-rudiment.
- » 19. The primary setae on a typical abdominal segment. Type I.
- » 20. Type Ia, the usual arrangement of the *Saturniidae*.
- » 21. Type Ib, the armature of some *Lymantridae*.  
For fig. 18, 19, 20, 21 see Chapter V, p. 42 sqq.

- » 22. *Hepialus hectus* Linn. Instar I, dorsal aspect,  
» 23. " " " " " lateral aspect.  
» 24. " " " " " ventral aspect.  
» 25. *Hepialus* cf. *lupulinus* Linn. Instar V, lateral aspect. Compare fig. 4 and 14.  
» 26. *Zeuzera pyrina* Linn. (*Cossidae*), mature larva. Coll. KALL. Pro-, meso- and metathorax, and abd. 1, 2, 3, lateral aspect.  
» 27. " " Pro-, meso- and metathorax, abd. 1, dorsal aspect.

## PLATE II.

- » 1. *Bombyx mori*. Instar I, newly hatched, dorsal aspect.  
» 2. " " " " " lateral aspect.  
» 3. " " " " just before moulting, lateral aspect.  
» 4. " " " II, just after moulting " "  
Mark the numerous secondary setae.  
» 5. " " Abdominal segment 5 of mature larva.  
Observe the primary verrucae between the secondary setae.  
» 6a, b. *Lasiocampa rubi* (*Lasiocampidae*). Prothorax, mesothorax and abd. segment 5 of Instar III.  
» 7. " " Abdominal segment 5 of mature larva.  
» 8. *Oncercia dispar* (*Liparidae*). Instar I, dorsal aspect.  
» 9. " " " " " lateral aspect.  
» 10. " " " " " the curious setae, which disappear after moulting.  
» 11a, b. " " " " " mature larva. Prothorax and 5th abdominal segment (see Type Ib, Plate I, fig. 21).  
» 12. *Porthesia chrysorrhoea* (*Liparidae*) Instar I, dorsal aspect.  
» 13. " " " " " lateral aspect.  
» 14. " " " " " mature larva. Pro- and mesothorax.  
» 15. " " " " " 6th abdominal segment.

## PLATE III.

- Fig. 1. *Orgyia antiqua* (*Liparidae*). Instar I, ventral aspect.  
 » 2. » » » » I, lateral aspect.  
 » 3. » » » » II, » »  
 » 4. » » » » III, » »  
 » 5. » » » » IV, pro-, meso- and metathorax,  
 abdominal segm. 1.  
 » 6. » » » » V, mature larva, partly after  
 J. HÜBNER (1786).

Fig. 1—6 show the ontogeny of the plumose setae and Type I b.

- » 7. *Phalera* (*Pygaera*) *bucephala* (*Notodontidae*). Instar I, lateral aspect.  
 » 8. » » » » Instar I, dorsal aspect.  
 » 9. » » » » » ventral aspect.  
 » 10. » » » » » II, lateral aspect.  
 » 11. » » » » » III, prothorax, mesothorax, abd.  
 segment 5.  
 » 12. » » » » » IV, prothorax, abd. segment 5.  
 » 13. » » » » » V, mature larva, abd. segment 5.

Fig. 7—13 show the development of stripes.

- » 14. *Saturnia pavonia*, Instar I. Type I a.  
 » 15. » » » » V, mature larva, 5th abd. segment.

## PLATE IV.

- » 1. *Sphinx ligustri*. Instar I, lateral aspect.  
 » 2a, b. *Smerinthus tiliae*. Instar I, lateral aspect.  
 » 3a, b. *Smerinthus populi*. Instar I, » »

Fig. 1—3 show the primary setae and the secondary forked ones.

Observe seta *prostigmatis*.

- » 4. *Arctia caja*. Instar I, lateral aspect.  
 » 5a, b. » » » » III, prothorax and 5th abdominal segment.  
 » 6. *Ocnogyna lubricipeda* (*Arctiidae*), mature larva.  
 » 7. *Euchelia jacobaea*. (*Arctiidae*) Instar I?, lateral aspect.

Fig. 4—7 show the development of the plumed setae and the occurrence of verrucae and primary setae in this family. Compare Plate I, fig. 5.

- » 8a, b. *Mamestra brassicae* (*Noctuidae*), prothorax, mesothorax and 5th  
 abdominal segment of mature larva.  
 » 9a, b. *Acronycta psi* (*Noctuidae*), metathorax, 1st and 8th abdominal  
 segments of mature larva.

Observe the origin of the fleshy horns from *v. dorsalis* and *v. subdorsalis*.

- » 10. *Depressaria nervosa* (*Noctuidae*). Coll. KALL. Note the arrangement  
 of the pigment-spots, according to Type I and  
 the absence of setae.

Compare with fig. 8, 9, 10, Pl. I, fig. 9, 10, 17.

- Fig. 11. *Thyris fenestrella*, mature larva. Coll. KALL., dorsal aspect.  
 » 12. » » » » » » ventral aspect.  
 » 13. » » » » » » lateral aspect.  
 » 14. *Vanessa urticae* (*Nymphalidae*). Instar I.  
 » 15. » » » mature larva, 5th abd. segment.

## PLATE V.

- » 1. *Pieris brassicae*. Instar I, newly hatched, dorsal aspect.  
 » 2. » » » » immediately before the moulting, lateral aspect.  
 » 3. » » » II, partly dorsal, partly lateral aspect.  
 » 4. » » » III, lateral aspect.  
 » 5a, b » » » IV, pro-, meso- and metathorax, 1st abd. segment; abd. segm. 2, 3, 4, 5, 6.  
 » 6a, b » » » V, pro-, meso- and metathorax, abd. segm. 5 of mature larva.  
 » 7. » » » Pupa, abdomen.

Compare Plate I, fig. 13. Observe the development of the chalazae from the primary setae, the origin of the stripes, the reduction of the pupal pigment-spots in comparison with the mature larva, and *v. dorsolateralis* on the pupa.

- » 8. *Pieris napi*. Instar I.  
 » 9. » » » II.  
 » 10a, b » » » III, pro- meso- and metathorax, 5th abd. segm.  
 » 11. » » » IV, abdom. 5.  
 » 12. » » » V, abdom. 5 of mature larva.  
 » 13. » » » Pupa, abdomen.

Observe the development of the secondary setae and the disappearance of the primitive arrangement.

The pupa has the same pattern as Instar I, with a well developed *s. dorsolateralis*. Note the increase of the pigment-spots in comparison with the mature larva.

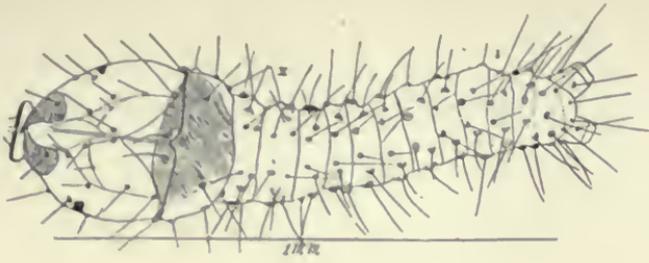
- » 14. *Sericinus telamon* (*Papilionidae*), mature larva.  
 Coll. Kall. Pro-, meso- and metathorax, abdom. 1.  
 Observe the osmaterium on the place of *v. dorsalis*.

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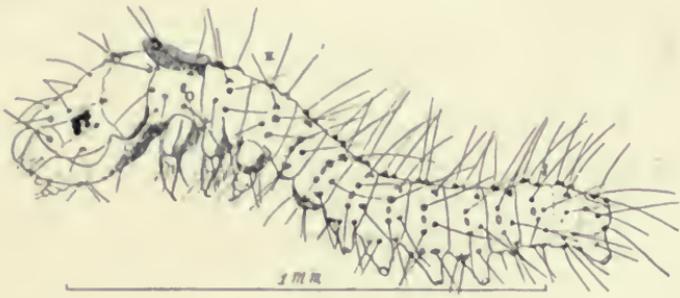
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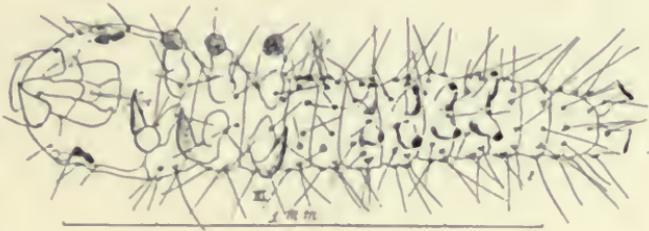
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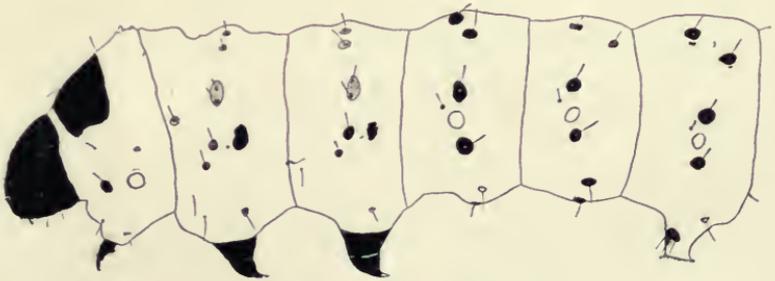
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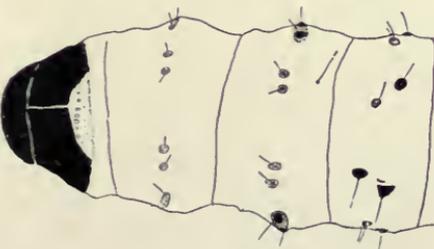
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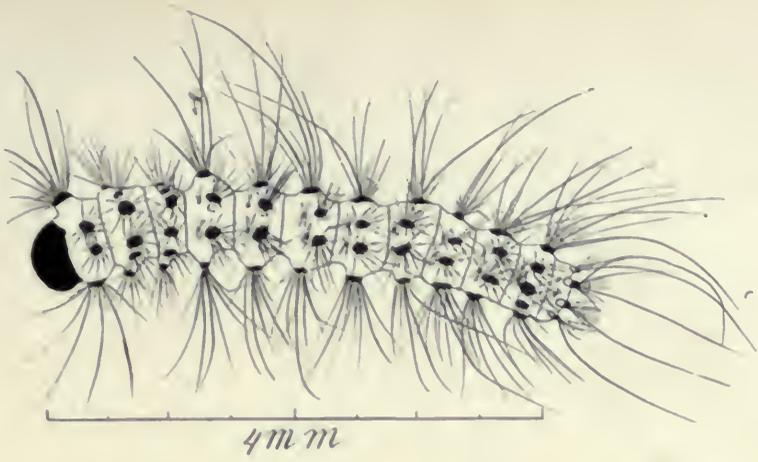




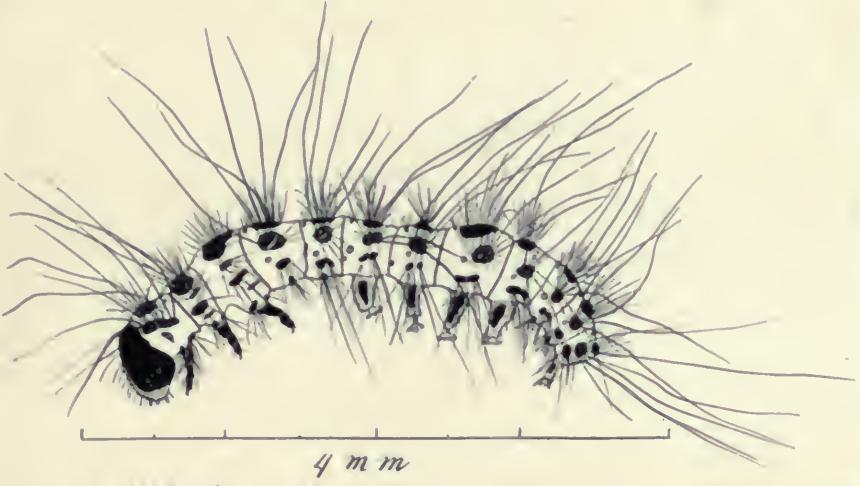




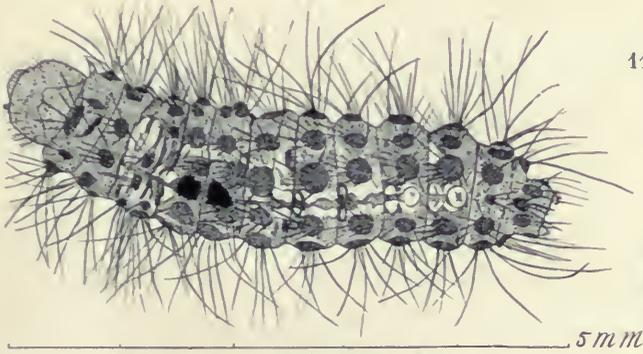
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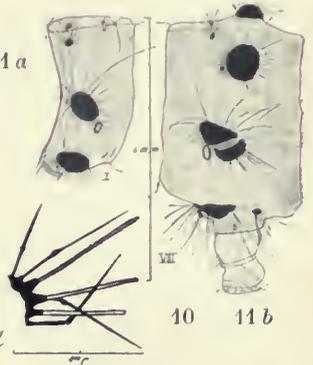
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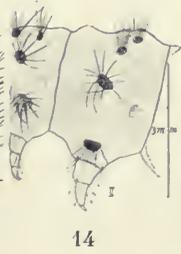
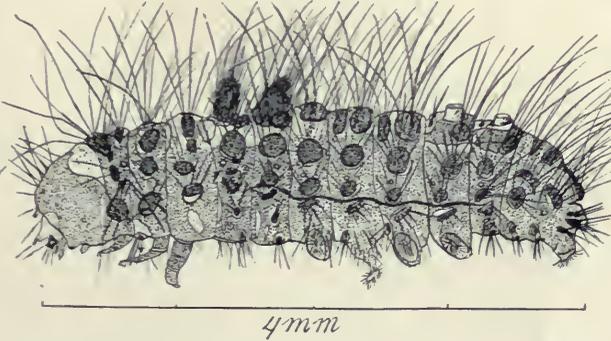
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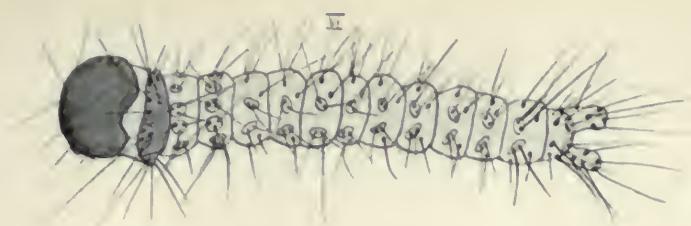
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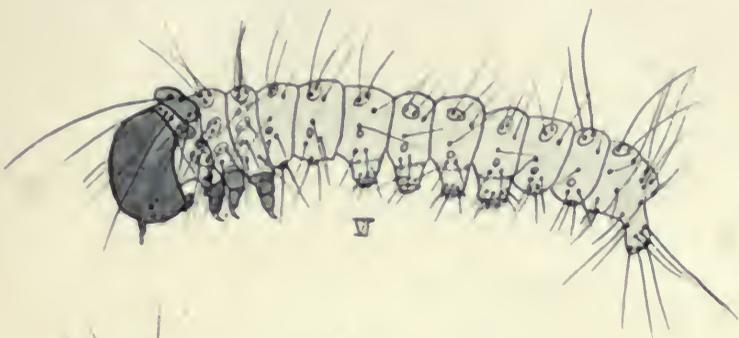




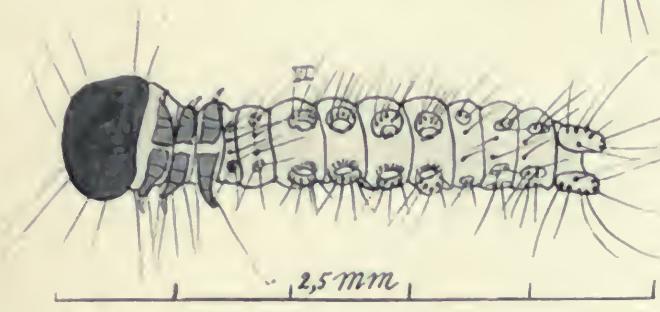
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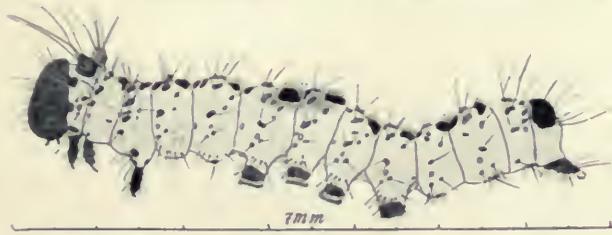


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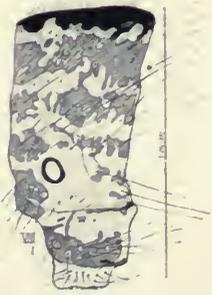
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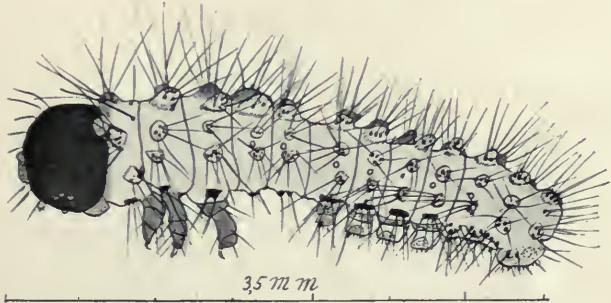


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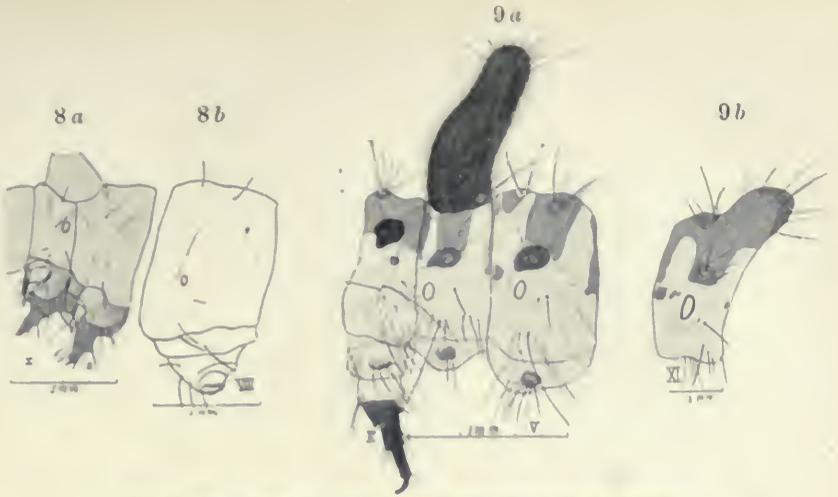
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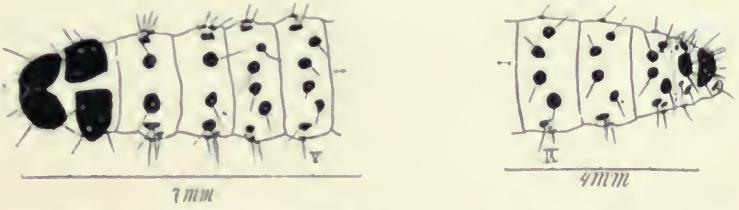




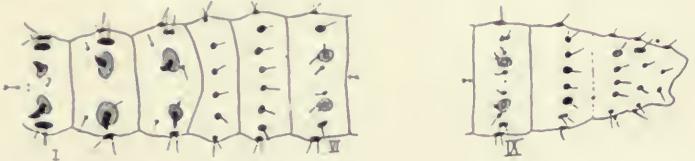
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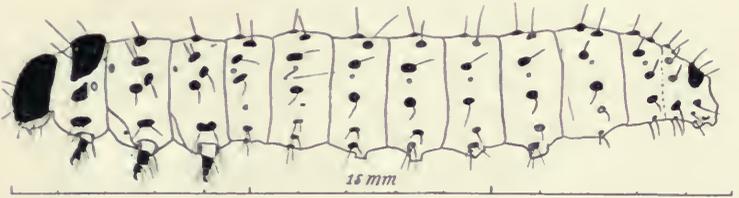
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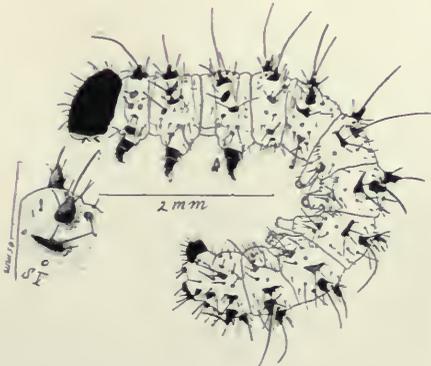
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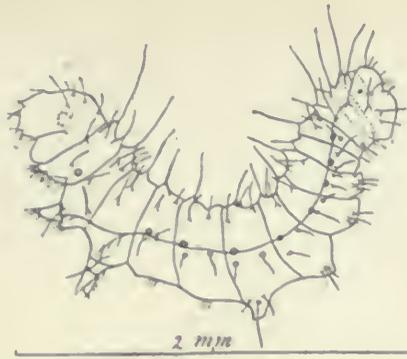




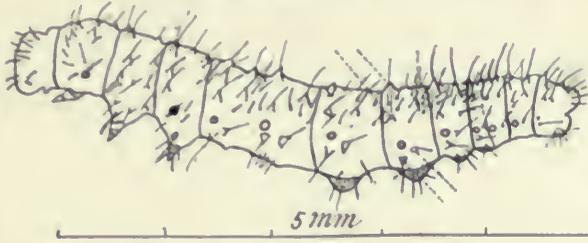




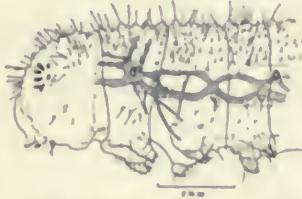
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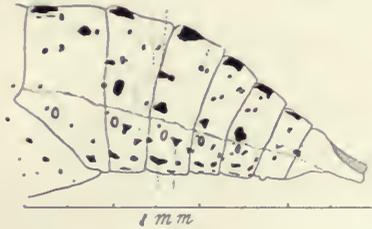
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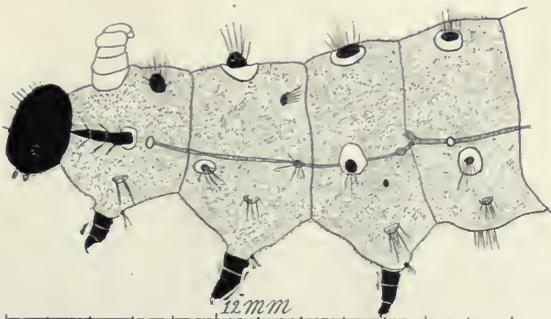
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STELLINGEN.



## STELLINGEN.

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### I.

De excretie-organen van *Amphioxus* zijn geen protonephridiën.

### II.

De bewering van *VON HESZ*, dat de bijen kleurenblind zijn, is door *VON FRISCH* afdoende weerlegd.

### III.

De meening van *DICKEL*, dat jonge bijenlarven hermaphrodiet zijn en door de voeding veranderd kunnen worden in darren of wijfjes, is onjuist.

### IV.

De redenen, door *FABRE* aangevoerd om de doofheid der Cicaden aan te toonen, zijn geen bewijzen.

### V.

De laterale kelkbladeren der Cruciferen zijn de buitenste.

### VI.

De alcoholgisting van *Saccharomyces* is slechts voor een gering gedeelte toe te schrijven aan een zuivere fermentwerking.

## VII.

Het voorkomen van chitine bij verschillende planten wijst niet op een systematische verwantschap.

## VIII.

De bewering van STEINMANN, dat de Delphinidae afstammen van de Ichthyosauria, is ongegrond.

## IX.

De wet van de toeneming der lichaamsgrootte is in strijd met de waarneming.

## X.

Drijftillen zijn gunstig voor de veenvorming.

## XI.

Het is wenschelijk, dat zoo spoedig mogelijk het ius promovendi aan de bezitters van een einddiploma eener Hoogere Burgerschool met vijf-jarigen cursus wordt verleend.

## XII.

Het normaalprogramma voor de Rijks Hoogere Burgerscholen met vijfjarigen cursus is in strijd met de wet van 1863, art. 17e.

## XIII.

Bij het onderwijs op een Hoogere Burgerschool met vijfjarigen cursus dient de historische geologie door den leeraar in de natuurlijke historie, de algemeene geologie door den leeraar in de aardrijkskunde te worden behandeld.

## XIV.

Het is wenschelijk de hoofdpunten der physiologie en der mikroskopische anatomie van planten en dieren op een Hoogere Burgerschool met vijfjarigen cursus te behandelen.

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