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STUDIES IN THE THEORY OF DESCENT, VOLUME II

August Weismann

Studies in the Theory of Descent, Volume II

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Содержание

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I. Larva and Imago vary in Structure independently of each other

It would be meaningless to assert that the two stages above mentioned were *completely* independent of one another. It is obvious that the amount of organic and living matter contained in the caterpillar determines the size of the butterfly, and that the quantity of organic matter in the egg must determine the size of the emergent larva. The assertion in the above heading refers only to the structure; but even for this it cannot be taken as signifying an absolute, but only a relative independence, which, however, certainly obtains in a very high degree. Although it is conceivable that every change of structure in the imago may entail a correlative change of structure in the larva, no such cases have as yet been proved; on the contrary, all facts indicate an almost complete independence of the two stages. It is quite different with cases of *indirect* dependence, such, for example, as are brought about by 'nurse-breeding.' This phenomenon is almost completely absent in Lepidoptera, but is found in Diptera, and especially in Hymenoptera in every degree. The larvæ of ichneumons which live in other insects, require (not always, but in most instances) that the female imago should possess a sharp ovipositor, so that in this case also the structure and mode of life of the larva influences the perfect insect. This does not depend, however, on inherent laws of growth (correlation), but on the action of external influences, to which the organism endeavours to adapt itself by natural selection.

I will now let the facts speak for themselves.

It is shown by those species in which only one stage is di- or polymorphic that not every change in the one stage entails a corresponding change in the other. Thus, in all seasonally dimorphic species we find that the caterpillars of butterflies which are often widely different in the colour and marking of their successive generations are absolutely identical. On the other hand, many species can be adduced of which the larvæ are dimorphic whilst the imagines occur only in one form (compare the first and second essays in this volume).

There are however facts which directly prove that any one stage can change independently of the others; I refer to the circumstance that any one stage may become independently variable – that the property of greater variability or of greater constancy by no means always occurs in an equal degree in all the three stages of larva, pupa, and imago, but that sometimes the caterpillar is very variable and the pupa and imago quite constant. On the other hand, all three stages may be equally variable or equally constant, although this seldom occurs.

If variability is to be understood as indicating the period of re-modelling of a living form, whether in its totality or only in single characters or groups of characters, from the simple fact of the heterochronic variability of the ontogenetic stages, it follows that the latter can be modified individually, and that the re-modelling of one stage by no means necessarily entails that of the others. It cannot however be doubted that variability, from whatever cause it may have arisen, is in all cases competent to produce a new form. From the continued crossing of variable individuals alone, an equalization of differences must at length take place, and with this a new, although not always a widely deviating, constant form must arise.

That the different stages of development of a species may actually be partly variable and partly constant, and that the variable or constant character of one stage has no influence on the other stages, is shown by the following cases, which are, at the same time, well adapted to throw light on the causes of variability, and are thus calculated to contribute towards the solution of the main problem with which this investigation is concerned.

When, in the following pages, I speak of *variability*, I do not refer to the occurrence of local varieties, or to variations which occur in the course of time, but I mean a high degree of individual variability – a considerable fluctuation of characters in the individuals of one and the same district or of the same brood. I consider a species to be constant, on the other hand, when the individuals from a small or large district differ from one another only to a very slight extent. Constant forms are likewise generally, but not invariably, such as are poor in local varieties, whilst variable forms are those which are rich in such variations. Since the terms "variable" and "constant" are but relative, I will confine myself to the most extreme cases, those in which the individual peculiarities fluctuate within very wide or very narrow limits.

As no observations upon the degree of variability shown by a species in the different stages of its development were available, I was obliged to fall back upon my own, at least so far as relates to the larval and pupal stages, whilst for the imaginal stage the wide experience of my esteemed friend Dr. Staudinger has been of essential service to me.

Let us in the first place confine our attention to the three chief forms which every Lepidopteron presents, viz. larva, pupa, and imago. With respect to the constancy or variability of these three forms, we actually find in nature all the combinations which are theoretically conceivable.

(1.) There are species which possess a high degree of constancy in all three stages, such, for example, as *Limenitis Camilla*, *Pieris Brassicæ*,[1] *Sphinx Ligustri*, and *Euchelia Jacobææ*.

(2.) There are species showing a high degree of variability in all three stages. This case must be of rare occurrence, as I am only able to adduce *Araschnia Prorsa-Levana*, a fact which arises from the circumstance that the pupal stage is, as a rule, but seldom variable.

(3.) There are species which are variable in two stages and constant in the third. To this class, for example, belongs *Smerinthus Tiliæ*, of which the larva and imago are very variable, whilst the pupa is quite constant. The same is the case with *Lasiocampa Pini*, the well-known fir moth. Many butterflies show this same phenomenon in other combinations, such, for instance, as *Vanessa Urticæ* and *Polychloros*, in which the larva and pupa are very variable, and the imago very constant. In a less degree the same is also the case with *Vanessa Atalanta*, whilst in *Pieris Napi* the pupa and imago are variable, and the caterpillar remarkably constant, this likewise being the case with the local form *Bryoniæ*, which, according to my theory, is to be regarded as the parent form of *Napi* (See Part I. of the present volume).

(4.) There are species which are constant in two stages, and variable only in the third. Thus, a few species can be found in which the larva and pupa are constant and the imago variable. This is the case with *Saturnia Yamamai*, the imago of which is well known to present numberless shades of colour, varying from light yellow to greyish black, whilst the green caterpillar shows only slight individual differences of marking, and scarcely any differences of colour. The pupa of this species is quite constant. *Arctia Caja* and *Hebe*, and *Chelonia Plantaginis* belong to this same category.

There are a very large number of species which possess very constant imagines and pupæ, but extremely variable larvæ. The following are the cases known to me: —*Macroglossa Stellatarum*, *Fuciformis* and *Bombyliformis*; *Chærocampa Elpenor*, *Celerio*, and *Nerii*; *Deilephila Galii*, *Livornica*, Hübn., *Hippophaës*, *Vespertilio*, and *Zygophylli*; *Sphinx Convolvuli*; *Acherontia Atropos*; *Smerinthus Ocellatus* and *Tiliæ*; *Callimorpha Hera*; *Cucullia Verbasci* and *Scrophulariæ*.

Cases in which the variability depends entirely upon the pupa, while the larva and imago are extremely constant, are of great rarity. *Vanessa Io* is a case in point, the pupa being light or dark

[1] [The slight variability in the colour of this pupa, opens up the interesting question of the photographic sensitiveness of this and other species, which is stated to cause them to assimilate in colour to the surface on which the larva undergoes its final ecdysis. Some experiments upon this subject have been recorded by Mr. T. W. Wood, Proc. Ent. Soc. 1867, p. xcix, but the field is still almost unexplored. R.M.]

brown, or bright golden green, whilst in the two other stages scarcely any light shades of colour or variations in the very complicated marking are to be met with.

The facts thus justify the above view that the individual stages of development change independently – that a change occurring in one stage is without influence on the preceding and succeeding stages. Were this not the case no one stage could possibly become variable without all the other stages becoming so. Did there exist a correlation between larvæ, pupæ, and imagines of such a nature that every change in the larva entailed a corresponding change in the imago, as soon as a large number of larval characters became fluctuating (*i. e.* as soon as this stage became variable), a large number of imaginal characters would necessarily also become fluctuating (*i. e.* this stage would also become correspondingly variable).

There is one other interpretation which might perhaps be attempted from the point of view of the old doctrine of species. It might be said that it is a special property of certain larval or imaginal markings to be variable whilst others are constant, and since the larval and imaginal markings of a species are generally quite distinct, it may easily happen that a butterfly possessing markings having the property of constancy may belong to a caterpillar having variable markings.

There is a soul of truth underlying this objection, since it is true that the various forms of markings which occur in Lepidoptera apparently reach different degrees of constancy. If we speak of the constancy or variability of a species, a different meaning is attached to these expressions according as we are dealing *e. g.* with a species of *Sphinx* or a species of *Arctia*. That which in the latter would be estimated as a high degree of constancy, in the former would be taken as a considerable amount of variability. It is of interest, in connection with the question as to the causes of constancy, to note that the power of any form of marking to attain to a high degree of constancy is by no means inversely proportional to the complication of the marking, as would have been expected *à priori*.

Thus, the species of *Sphinx* and of allied genera possess on their fore-wings, which are mostly coloured with a mixture of dull grey, white and black, an exceedingly complicated arrangement of lines which, in constant species, show a high degree of uniformity: on the other hand, the checquered fore-wings of our *Arctiidæ*, which are far more coarsely marked, always show, even in the most constant species, well-marked individual differences. The different types of marking must therefore be measured by different standards.

But in granting this, we decidedly refute the statement that constancy and variability are inherent properties of certain forms of marking.

This reasoning is based on the simple fact that a given type of marking comprises both species of great constancy and of (relatively) great variability.

Thus, the fore-wings of *Sphinx Ligustri* and *S. Convolvuli* are extremely constant, whilst the very similarly marked *Anceryx (Hyloicus) Pinastri* is exceedingly variable. Similarly *Deilephila Euphorbiæ* is known by its great variability of colouring and marking, whilst *D. Galii*, which resembles this species so closely as to be sometimes confounded with it, possesses a high degree of constancy, and further, the Corsican and Sardinian *D. Dahlii* is very variable. Among the family *Arctiidæ*, *Callimorpha Hera* and the Alpine *Arctia Flavia* are cases of constancy, whilst *A. Caja*, which is so similar to the last species, is so generally variable that two perfectly identical specimens can scarcely be found together.

The same can be shown to hold good for the markings of caterpillars. Thus, the larva of *D. Dahlii* shows very considerable variability, whilst that of *D. Galii* is very constant in marking (disregarding the ground-colour). So also the larva of *Vanessa Urticæ* is very variable and that of *V. Antiopa* very constant, &c.

The great differences with respect to constancy or variability which are displayed by the different stages of one and the same species, must therefore find their explanation elsewhere than in the type of the marking itself. The explanation must be found in the circumstance that each stage changes independently of the others, and at different periods can enter a new phase of variability.

We are here led in anticipation to the main question: – Are changes produced by internal or external causes? is it the physical nature of the organism which is compelled to become remoulded spontaneously after the lapse of a certain period of time? or does such modification only occur when produced directly or indirectly by the external conditions of life?

In the cases before us the facts undoubtedly indicate a complete dependence of the transformations upon external conditions of life.

The independent appearance of variability in the separate stages of the metamorphosis might, however, be regarded as only apparent. It might still be attempted to attribute the changes to a purely inherent cause, *i. e.*, to a phyletic vital force, by assuming that the latter acts periodically in such a manner that at first one and then the following stage becomes variable, until finally the entire species is transformed.

There is but little to be said in reply to this if we once take refuge in entirely unknown forces, the operation of which can be arbitrarily conceived to be either constant or periodic.

But granting that such a transforming power exists and acts periodically, the variability must always pass over the different stages in a fixed direction, like a wave over the surface of water – imago, pupa, and larva, or larva, pupa, and imago, must *successively* become variable. Cases like that of *Araschnia Prorsa*, in which all three stages are variable, may certainly be thus explained, but those instances in which the larva and imago are extremely variable, and the pupa quite constant, are entirely inexplicable from this point of view.

The latter can, however, be very simply explained if we suppose the changes to be dependent upon external influences. From this standpoint we not only see how it is possible that an intermediate stage should remain uninfluenced by the changes which affect the two other stages, but we can also understand why it should just be the pupal stage that plays this part so frequently. If we ask why most pupæ are constant and are relatively but very slightly variable, the answer will be found in the facts that all pupæ which remain concealed in the earth or inside plants (*Sesiidæ*), or which are protected by stout cocoons, show complete constancy, whilst any considerable amount of variability occurs only in those pupæ which are suspended or openly exposed. This is closely connected with a fact to which I have called attention on a former occasion,[2] viz., that dimorphism occurs in certain pupæ, but only in those which are openly exposed and which are therefore visible to their foes. I am only acquainted with such cases among the pupæ of butterflies, and it is likewise only among these that I have found any considerable amount of variability.

Facts of this kind indicate that Nature does not uselessly sport with forms, but that at any rate changes of this sort result from external influences. The greater frequency of variability among larvæ and its comparative rarity in imagines is also undoubtedly in favour of this view.

It has already been shown that species with variable larvæ and constant imagines are extremely common, but that those with constant larvæ and variable imagines are very rare. This confirms the conclusions, already drawn above, first, that the variability of the imago cannot owe its existence to the variability of the larvæ, and secondly, that the causes which produce variability affect the larval condition more commonly than that of the imago.

Where can these causes be otherwise sought than in the external conditions of life, which are so widely different in the two stages, and which are much more variable for the larva than for the imago?

Let us take the species of one genus, *e. g.* those of *Deilephila*. The imagines of our European species – as far as we know – all live in precisely the same manner; they all fly at twilight,[3] showing a preference for the same flowers and very often frequenting the same spots, so that in the haunts of one species the others are almost always to be met with, supposing them to occur in the same locality. They conceal themselves by day in similar places, and are attacked by similar foes.

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[2] "Über den Einfluss der Isolirung auf die Artbildung." Leipzig, 1872, p. 20.

[3] In some instances *Deilephila Lineata* has also been seen by day hovering over flowers.

It is quite different with the caterpillars. These, even in the case of the most closely allied species, live under different conditions, as appears from the fact that they feed on different plants. The latter can, however, produce changes both directly and indirectly. The larvæ may acquire adaptive colours and markings, and these would vary in accordance with the colour and structure of the food-plant; or they may become brightly coloured as a sign of distastefulness in cases where they are inedible. Then again the colour of the soil on which the larvæ live would act upon their colours making these adaptive. Certain habits of the caterpillars may also be dependent upon the nature of their food-plants. Thus, *e. g. Deilephila Hippophaës* feeds only at night, and conceals itself by day under moss and among the leaves at the base of the food-plant; but *D. Euphorbiæ* could not acquire such a habit, because *Euphorbia Cyparissias* generally grows on arid soil which is poor in vegetation, and which therefore affords no concealment, and furthermore, because a caterpillar, as long as it continues to feed, cannot, and as a matter of fact does not, ever wander far from its food-plant. A habit of concealment by burying in the earth also, such for example as occurs in *Acherontia Atropos*, could not be acquired by *D. Euphorbiæ*, because its food-plant generally grows on hard, dry, and stony ground.

In addition to these considerations, the foes would be different according as the caterpillar lived on plants which formed dense thickets covering large extents of the shore (*Hippophae*) or grew isolated on dry hillocks and declivities where the herbage was scanty or altogether absent; or again, according as the insect, in conjunction with such local differences, fed by day or had acquired the habit of feeding only by night. It must in fact be admitted that new and improved adaptations, or, in more general terms, that inducements to change, when depending on the environment, must be more frequently dissimilar for larvæ than for the imagines. We must accordingly expect to find actual change, or that condition of variability which may be regarded as initiative to change, occurring more commonly in larvæ than in perfect insects.

Since facts are in complete accordance with the results of these *à priori* considerations we may also venture to conclude that the basis of the considerations is likewise correct, viz., the supposition that the changes of colour and marking in caterpillars, pupæ, and imagines result from external influences only.

This must not be taken as signifying that the single stages of the larval development are also only able to change through the action of external influences. The larval stages are correlated with each other, as has already been shown (see the previous essay): new characters arise in the adult caterpillar at the last stage and are then gradually transferred back to the younger stages quite independently of external influences, this recession being entirely brought about by the laws of correlation. Natural selection here only exerts a secondary action, since it can accelerate or retard this transference, according as the new characters are advantageous or disadvantageous to the younger stages.

Now as considerable individual differences appear in the first acquisition of a new character with respect to the rapidity and completeness with which the individuals acquire such a character, the same must obtain for the transference of an improvement acquired in the last stage to the next younger stage. The new character would be acquired by different individuals in different degrees and at different rates – it would have, to a certain extent, to struggle with the older characters of the stage; in brief, the younger stage would become variable.

Variability of this kind might well be designated as *secondary*, in contradistinction to *primary* variability; the latter (primary) depends upon an unequal reaction of the individual organisms to external influences, the former (secondary) results from the unequal strength and rate of the action of the innate laws of growth governing the organism. In both cases alike exceeding variability may occur, but the causes producing this variability are dissimilar.

The different stages of larval development would thus frequently display independent variability in a manner similar to the pupal or imaginal stages, since they can show individual variability while the other stages of development remain constant. This appearance of independent variability in the different stages of the larval development, however, is in truth deceptive – we have here in fact a kind of wave of variability, which passes downwards through the developmental stages, becoming gradually weaker, and finally dying out completely.

In accordance with this, we very frequently find that only the last or two last stages are variable, while the younger stages are constant. Thus in *Macroglossa Stellatarum*, the larvæ are constant in the first, second, and third stages, but become variable in the fourth, and in the fifth stage first show that high degree of variability which has already been described in detail (See. Pl. III., Figs. 3–12). The larvæ, of *Vanessa Cardui* also, according to my notes, are extremely constant in the first four stages in spite of their complicated marking, but become variable in the fifth stage, although to no very great extent.

In *Smerinthus Tiliæ*, *Ocellatus* and *Populi* also, the greatest larval variability is shown only in the last stage, the preceding stages being very constant. These cases by no means depend upon the marking of the young stages being simpler and therefore being less capable of varying. The reverse case also occurs. In a somewhat similar manner as the young of the tapir and wild hog are striped, while the adult animals are plainly coloured, the young caterpillars of *Saturnia Yamamai* possess longitudinal black lines on a yellow ground, while as early as in the second stage a simple green colour appears in the place of this complicated but perfectly constant marking. If the young stages are so frequently constant, this rather depends upon the fact that the transference of a new character to these stages not only takes place gradually, but also with continually diminishing energy, in a manner somewhat similar to physical motion, which continually diminishes in speed by the action of resistance till it is completely arrested. This constancy of the younger stages may further be due to the circumstance that the characters would only be transferred when they had become fixed in the last stage, and were consequently no longer variable. The transferred characters may thus have acquired a greater regularity, *i. e.* a less degree of variability, than they possessed at their first origination. Extensive investigations in this special direction must be made if the precise laws, in accordance with which the backward transference of new characters takes place, are to be discovered. By such researches only should we arrive with certainty at the causes which determine the lesser variability of the young larval stages.

It may also occur that the early stages are variable, whilst the later stages are constant, although this case appears to happen less frequently. Thus, the caterpillars of *Gastropacha Quercifolia* vary considerably in the second stage but are constant at a later period, and the same is the case with *Spilosoma Urticæ*, which in the second stage may be almost considered to be dimorphic, but which subsequently becomes constant.

Cases in which the first stage is variable appear to be of the least frequent occurrence. I know of only one such instance, viz., *Anceryx Pinastri*, of which the newly hatched larvæ (Pl. VI., Fig. 53) show considerable differences in the brownish-black crescentic spots. The second (Fig. 54), third, and fourth stages are then tolerably constant, while the fifth stage again is very variable.

An instance of this kind can be easily explained by two waves of variation, the first of which now affects only the first stage, while the second has just commenced to affect the fifth stage. Such a supposition is not opposed to any theoretical considerations, but rather has much probability in its favour, since we know that species are from time to time subject to be remodelled; and further, that the coalescence of several stages of phyletic development in the ontogeny of one and the same species (see p. 226, development of the genus *Deilephila*) shows that during the backward transference of one character, new characters may appear in the last stage of the ontogeny, and indeed very frequently at a time when the next youngest character has not been transferred back so far as to the first stage.

That this secondary variability is to a certain extent brought about by the conflict between the old and new characters, the latter striving to suppress the former, is shown by the caterpillar of *Saturnia Carpini* which I have observed for many years from this point of view, and than which I do not know a more beautiful illustration.

When these larvæ leave the egg they are black, but in the adult state are almost bright green – this at least being the case in a local form which, from the district in the vicinity of Genoa where it is found, I will designate as the var. *Ligurica*. Now whilst these two extreme stages of development are relatively constant, the intermediate stages show a variability which becomes greater the nearer the last stage is approached, this variation in the marking depending simply on the struggle between the green colour and the more anciently inherited black. In this manner there arises, especially in the fourth stage of the German local form, an incredible mixture of the most diverse markings, all of which can, however, be very easily explained from the foregoing point of view.

The simpler and, as I am inclined to believe, the older form of the transformation is presented to us in the local variety *Ligurica*. In the last stage, when 7.5 centimeters long, this form is of a beautiful bright green colour without any trace of black marking[4] (Pl. VIII., Fig. 77). The colour of the six orange warts which are situated on each segment is also similar in all specimens, so that this stage is perfectly constant.

Our German *S. Carpini* shows different characters in the fifth stage. It is true that individual specimens occur which are entirely green without any black, but these are rare; the majority possess a more or less broad black ring encircling the middle of each segment (Pl. VIII., Figs. 78 and 79). Those specimens in which the black ring has become broken up into large or small spots surrounding the base of the warts constitute intermediate forms (Fig. 80). The last stage of the German local form, unlike that of the Genoese local form, is therefore very variable.

The two forms, moreover, do not simply differ in being more or less advanced in phyletic development, but also in several other points. As it is of great theoretical interest to show that a species can develop local differences only in the stage of larva, I will here subjoin the plain facts.

The differences consist in that the Genoese local form goes through five moults whilst the German local form, like most caterpillars, has only four moults. Further, in the Genoese form the light green, which is also possessed by the German form in the fourth stage, when it once appears, is retained to the end of the larval development, whilst in the fifth stage of the German form this colour is replaced by a dull greyish-green (compare Figs. 77 and 78). There is further a very considerable difference in the earlier stages which shows that the phyletic transforming process has taken a quite independent course in the two forms. Since the struggle between the green and black – retaining this idea – appears to be quite finished in the last stage of the Genoese form, we should expect that the new colour, green, would now also have encroached further upon the younger stages than in the German form. Nevertheless, this is not the case, but quite the reverse happens, the black maintaining its ground longer in the Italian than in the German form.

In the Genoese form the two first stages are completely black, and in the third stage an orange-yellow lateral stripe first appears. In the German form this stripe appears in the second stage, and there is not subsequently added, at least on the middle segments, a yellow border surrounding some of the warts of the median series. In the third stage, however, the yellow (which is but the precursor of the later green colour) becomes further extended, so that the caterpillars often appear of an orange colour, some or all of the warts and certain spots and stripes only being black (Figs. 66 and 68). The warts are also often yellow while the ground remains in most part black – in brief, the bright colour is in full struggle with the black, and an endless series of variations is the result of this conflict, whilst in the corresponding stage of the Genoese form almost complete constancy prevails.

This constancy remains also in the following (fourth) stage, the caterpillar still being deep black, only the yellow (sulphur-coloured) lateral stripe, which has now become brighter, indicating the impending change (Fig. 67). This takes place in the fifth stage, in which the ground-colour

[4] It is true that I only reared one brood, but from this fifty specimens were obtained. It would be interesting to know whether this variety of the caterpillar is distributed over the whole of Southern Europe.

suddenly becomes bright green, the black remaining at most only in traces on the anterior edges of the segments.

This is the same marking as is shown by the fourth stage of the German form, only in this case individuals quite destitute of black do not occur. In many specimens indeed black forms the ground-colour, the green only appearing in certain spots (Figs. 71 to 75); in others the green predominates, and these two extremes are connected by innumerable intermediate forms, so that this stage must be regarded as the most variable of all.

The sixth stage of the Genoese and the fifth of the German form have already been compared together. The results may be thus tabulated: —

A. German form. B. Genoese form.

Stage I. 9 days. Black; constant. 9 days. Black; constant.

Stage II. 8 days. Black, with orange-yellow lateral stripe; variable. Black, with yellow; very variable. 11 days. Black; constant.

Stage III. 5 days (in some cases as much as 16 days). 12 days. Black, with orange-yellow lateral stripes; constant.

Stage IV. 16 days (in some cases only 5 days). Bright green and black mixed; very variable. 6 days. Black, with bright yellowish lateral stripe; constant.

Stage V. 6 days (frequently longer). Dark green, with or without black bands; variable. 6 days. Bright green, small traces of black; variable.

Stage VI. Pupation. 18 days. Bright green, without any black; constant.

Stage VII. Pupation.

From this comparison we perceive that the process of transformation has at least become preliminarily concluded in the Genoese form. Why the backward transference of the newly-acquired character to the young stages has not yet occurred, or, at least, why it is not in progress, does not appear; neither can it be stated whether this will take place later, although we may venture to suppose that such will be the case. At first sight but a relatively short time appears necessary for the single stage V., which is still in a state of fluctuation (variable), to become constant by continued crossing, like all the other stages.

That the transformation is still in full progress in the German form, is shown by the fact that in this case all the stages are variable with the exception of the first – the second stage being only variable to a small extent, the third to a much greater extent, and the fourth to the highest degree conceivable, whilst the fifth and last stage is again less variable – so that the greatest struggle between the old and new characters takes place in the fourth stage.

Among the innumerable variations presented by this last stage a complete series of transitional forms can be arranged so as to show the gradual conquest of the black by the green, and thus indicating, step by step, the course which the latter colour has taken.

In the blackest specimens there is nothing green but the lateral (infra-spiracular) line which was yellow in the preceding stage, and a crescent-shaped streak at the base of the middle warts together with a still smaller crescent at the base of the upper warts (Figs. 71 and 81). These spots become extended in lighter specimens and approximate so as to leave only narrow black bridges, a third spot being added at the posterior edge of the warts (Figs. 72 and 82). The three spots then extend on all sides, still leaving for a long period narrow black lines at the boundaries where their growth has caused them to abut. In this manner there frequently arises on the green ground a true hieroglyphic-like marking (Figs. 85 and 86). Finally the black disappears from the anterior edge and diminishes on the middle line of the back where it still partly remains as a T-shaped figure (Figs. 73 and 74), although generally replaced elsewhere by the green with the exception of small residues.

One point remained for a long time inexplicable to me, viz., the change of the light green into dark grey-green which appeared in the last stage in connection with a total change of the black marking.

Supposing that new characters are actually acquired only in the last stage, and that from this they are transferred to the younger stages, we should expect to find completely developed in the last stage the same colouring and markings as are possessed more or less incompletely in the fourth stage. Now since the developmental tendency to the removal of black and to the predominance of green – if we may thus venture to express it – is obvious in the fourth stage, we may expect to find in the fifth stage a bright green ground-colour, either without any mixture of black or with such black spots and streaks as were retained in the fourth stage as residues of the original ground-colour. But instead of this the fifth stage shows a dark green colour, and a more or less developed black marking which cannot in any way be derived from that of the fourth stage.

The Genoese local form observed last year first gave me an explanation to the extent that in this form the last stage is actually only the potential penultimate stage, or, more correctly expressed, that the same characters which at present distinguish the last stage of this form, are already more or less completely transferred to the penultimate stage.

The apparently paradoxical behaviour of the German form can be explained by supposing that before the pure bright green had become completely transferred to the penultimate stage a further change appeared in the last stage, the green ground-colour becoming darker, and black transverse bands being formed. The marking of the last stage would then be regarded as the reverse of that of the preceding stage; the absence of black would be the older, simple black spots at the base of the warts the next in succession, and a connected black transverse band the most advanced state of the development.

Whether this explanation is correct, and if so, what causes have produced the second change, may perhaps be learnt at some future time by a comparison with the ontogeny of other *Saturniidæ*; in the meantime this explanation receives support from another side by the behaviour of the Genoese local form. If the last stage of the German form has actually commenced to be again re-modelled, then this variety is further advanced in phyletic development than the Genoese form; and this corresponds entirely with the theory that in the former the light colour (the orange considered as preliminary to the transformation into green) has already been carried down into the second stage, whilst in the Genoese variety even in the fourth stage only the first rudiments of the colour-transformation show themselves.

The Genoese form is to a certain extent intermediate between the German form of *Saturnia Carpini* and the nearly related *S. Spini*, a species inhabiting East Germany. In this latter the larvæ, even in the adult state, are completely black with yellow warts. This form of caterpillar must therefore be regarded as phyletically the oldest, and this very well agrees with the character of the moth, which differs essentially from *S. Carpini* only in not being sexually dimorphic. In *Carpini* the male possesses a far more brilliant colouring than the female, the latter agreeing so completely with the female of *Spini* that it can hardly be distinguished therefrom, especially in the case of the somewhat larger South European specimens of the last species. Now as the more simple colouring of the female must in any case be regarded as the original form, we must consider *Spini*, both sexes of which possess this colouring, to be phyletically the older form, and *Carpini*, the male of which has become differently coloured, must be considered as the younger type. This completely accords with the characters of the larvæ.

I must here mention that I have also asked myself the question whether the variations of the different larval stages are connected together as cause and effect – whether the lightest specimens of the fifth stage may perhaps not also have been the lightest individuals of the third and fourth stages.

Such relationship is only apparent between the third and fourth stages; the darkest larvæ of the third stage become the darker varieties of the fourth stage, although it is true that the lighter forms of the third sometimes also become dark varieties in the fourth stage. Between the fourth and fifth stages there is scarcely any connection of this kind to be recognized. Thus, the darkest varieties of the fourth stage sometimes become the lightest forms of the fifth stage, whilst in other cases from the lightest individuals of the fourth stage there arise all the possible modifications of the fifth stage.

Further details may be omitted: the negative result cannot cause any surprise, as it is a necessary consequence of the continued crossing that must take place.

We thus see that the three chief stages of development (larva, pupa, and imago) actually change in colour independently of each other, the single stages of the larval development being however in greater dependence upon one another, and being connected indeed in such a manner that a new character cannot be added to the last stage without being transferred in the course of time to the preceding stage, and at a later period from this again even to the youngest stage, supposing it not to be previously delayed in the course of its transference by unknown opposing forces. On this last point, however, the facts at present available do not admit of any certain decision.

But why do the individual larval stages behave in this respect so very differently to the chief stages of the whole development? why are the former so exactly correlated whilst the latter are not? If new characters have a general tendency to become transferred to the younger ontogenetic stages, why are not new imaginal characters first transferred to the pupa, and finally to the larva?

The answer to these questions is not far to find. The wider two stages of a species differ in structure, the less does correlation become possible; the nearer the two stages are morphologically related, the more powerful does the action of correlation become. It is readily conceivable that the more widely two succeeding stages deviate in structure and mode of life, the less possible does it become for characters to be transferred from one to the other. How is it possible, for example, that a new character in the proboscis or on the wings of a butterfly can be transferred to the caterpillar? If such correlation existed it could only manifest itself by some other part of the caterpillar changing in correspondence with the change of the proboscis or wings of the butterfly. That this is not the case has, in my opinion, been conclusively shown by all the foregoing considerations respecting the independent variability of the chief stages of the metamorphosis.

There are, moreover, an endless number of facts which prove the independence of the individual stages of development – I refer to the multitudinous phenomena presented by metamorphosis itself. The existence of that form of development which we designate as metamorphosis is alone sufficient to prove incontestably that the single stages are able to change independently of one another to a most remarkable extent.

If we now ask the question: how has the so-called "complete" metamorphosis of insects arisen? the answer can only be: through the gradual adaptation of the different stages of development to conditions of life which have continually deviated more and more widely from each other.[5]

But if individual stages of the post-embryonic development can finally attain to such complete diversity of structure as that of the larva and imago through gradual adaptations to continually diverging conditions of life, this shows that the characters acquired by the single stages are always only transferred to the same stages of the following generation, whilst the other stages remain uninfluenced thereby. This depends upon that form of heredity designated by Darwin "inheritance at corresponding periods of life," and by Haeckel "homochronic heredity."

[5] In this sense Lubbock says: – "It is evident that creatures which, like the majority of insects, live during the successive periods of their existence in very different circumstances, may undergo considerable changes in their larval organization in consequence of forces acting on them while in that condition; not, indeed, without affecting, *but certainly without affecting to any corresponding extent*, their ultimate form." – "Origin and Metamorphoses of Insects," London, 1874, p. 39.

II. Does the Form-relationship of the Larva coincide with that of the Imago?

Having thus established the independence in the variability of the individual stages of metamorphosis, I will now turn to the consideration of the question as to how far a parallelism is displayed in the phyletic development of these stages. Is there a complete congruence of form-relationship between larvæ on the one hand and imagines on the other? does the classification founded on the morphology of the imagines agree with that based on the morphology of the larvæ or not?

If, according to Claus,[6] we divide the order Lepidoptera into six great groups of families, it is at once seen that these groups, which were originally founded exclusively on imaginal characters, cannot by any means be so clearly and sharply defined by the larval characters.

This is certainly the case with the *Geometræ*, of which the larvæ possess only ten legs, and on this account progress with that peculiar "looping" movement which strikes even the uninitiated. This group, which is very small, is however the only one which can be founded on the morphology of the larvæ; it comprises only two nearly related families (*Phytometridæ* and *Dendrometridæ*), and it is not yet decided whether these should not be united into one group comprising the family characters of the whole of the "loopers."

Neither the group of Micro-lepidoptera, nor those of the *Noctuina*, *Bombycina*, *Sphingina*, and *Rhopalocera*, can be based systematically on larval characters. Several of these groups are indeed but indistinctly defined, and even the imagines present no common characteristics by which the groups can be sharply distinguished.

This is well shown by the *Rhopalocera* or butterflies. These insects, in their large and generally brilliantly coloured wings, which are usually held erect when at rest, and in their clubbed antennæ, possess characters which are nowhere else found associated together, and which thus serve to constitute them a sharply defined group.[7] The caterpillars, however, show a quite different state of affairs. Although the larval structure is so characteristic in the individual families of butterflies, these "larval-families" cannot be united into a larger group by any common characters, and the "*Rhopalocera*" would never have been established if only the larvæ had been known. It is true that they all have sixteen legs, that they never possess a Sphinx-like horn, and that they are seldom hairy, as is the case with many *Bombycidæ*,[8] but these common *negative* characters occur also in quite distinct groups.

In the butterflies, therefore, a perfect congruence of form-relationship does not exist, inasmuch as the imagines constitute one large group of higher order whilst the larvæ can only be formed into families. If it be admitted that the common characters of butterflies depend on their derivation from a common ancestor, the imagines must have retained certain common characters which enable them to be recognized as allies, whilst the larvæ have preserved no such characters from the period at which the families diverged.

Without going at present into the causes of these phenomena I will pass on to the consideration of further facts, and will now proceed to investigate both the form-relationships within the families. Here there can be no doubt that in an overwhelmingly large majority of cases the phyletic development

[6] "Grundzüge der Zoologie," 1875.

[7] [Lepidopterists are of course aware that even these distinctions are not absolute, as no single character can be named which does not also appear in certain moths. The definition in this case, as in that of most other groups of animals and plants, is only a general one. See, for instance, Westwood's "Introduction to the Classification of Insects," vol. ii. pp. 330–332. Also some remarks by C. V. Riley in his "Eighth Annual Report" on the insects of Missouri, 1876, p. 170. With reference to the antennæ as a distinguishing character, see Mr. A. G. Butler's article in "Science for All," 1880, part xxvii. p. 65. R.M.]

[8] The genus of *Morphinæ, Discophora*, possesses hairs very similar to those of the genus *Cnethocampa* belonging to the *Bombycidæ*.

has proceeded with very close parallelism in both stages; larval and imaginal families agree almost completely.

Thus, under the group *Rhopalocera* there is a series of families which equally well permit of their being founded on the structure of the larva or on that of the imago, and in which the larvæ and imagines therefore deviate from one another to the same extent. This is the case, for instance, with the families of the *Pieridæ*, *Papilionidæ*, *Danaidæ*, and *Lycænidæ*.

But there are also families of which the limits would be very different if the larvæ were made the basis of the classification instead of the butterflies as heretofore. To this category belongs the sub-family *Nymphalinæ*. Here also a very characteristic form of caterpillar indeed prevails, but it does not occur in all the genera, being replaced in some by a quite different form of larva.

In the latest catalogue of Diurnal Lepidoptera, that of Kirby (1871), 112 genera are comprised under this family. Of these most of the larvæ possess one or several rows of spines on most or on all the segments, a character which, as thus disposed, is not met with in any other family.

This character is noticeable in genera 1 to 90, if, from those genera of which the larvæ are known, we may draw a conclusion with reference to their allies. I am acquainted with larvæ of genus 2, *Agraulis*, Boisd. (*Dione*, Hübn.); of genus 3, *Cethosia*, Fabr.; 10, *Atella*, Doubl.; 12, *Argynnis*, Fabr.; 13, *Melitæa*,[9] Fabr.; 19, *Araschnia*, Hübn.; 22, *Vanessa*, Fabr.; 23, *Pyrameis*, Hübn.; 24, *Junonia*, Hübn.; 31, *Ergolis*, Boisd.; 65, *Hypolimnas*, Hübn. (*Diadema*, Boisd.); 77, *Limenitis*, Fabr.; 81, *Neptis*, Fabr.; 82, *Athyma*, Westw.; and finally with those of genus 90, *Euthalia*, Hübn. – which, according to Horsfield's figures, possess only two rows of spines, these being remarkably long and curved, and fringing both sides. It may be safely assumed that the intermediate genera would agree in possessing this important character of the Nymphalideous larvæ, viz., spines.

After the genus 90 there are 22 more genera, and these are spineless, at least in the case of the two chief genera, 93, *Apatura*, and 104, *Nymphalis*. Of the remainder I know neither figures nor descriptions.[10] In the two genera named the larvæ are provided with two or more spine-like tentacles on the head, and the last segment ends in a fork-like process directed backwards. The body is otherwise smooth, and differs also in form from that of the larvæ of the other *Nymphalinæ*, being thickest in the middle, and tapering anteriorly and posteriorly; neither is the form cylindrical, but somewhat flattened and slug-shaped. If therefore we were to arrange these butterflies by the larvæ instead of by the imagines, these two genera and their allies would form a distinct family, and could not remain associated with the 90 other Nymphalideous genera.

We have here a case of *incongruence*; the imagines of the genera 1–90 and 91–112 are more closely allied than their larvæ.

From still another side there arises a similar disagreement. The larvæ of the genera *Apatura* and *Nymphalis* agree very closely in their bodily form and in their forked caudal appendage with the caterpillars of another sub-family of butterflies, the *Satyrinæ*, whilst their imagines differ chiefly

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[9] [The larvæ of genera 14, *Phyciodes*, and 35, *Crenis*, are likewise spiny. See Edwards' "Butt. of N. Amer." vol. ii. for figures of the caterpillar of *Phyc. Tharos*: for notes on the larvæ of *Crenis Natalensis* and *C. Boisduvali* see a paper by W. D. Gooch, "Entomologist," vol. xiv. p. 36. The larvæ of genus 55, *Ageronia*, are also spiny. (See Burmeister's figure of *A. Arethusa*, "Lép. Rép. Arg." Pl. V. Fig. 4). The larvæ of genus 98, *Aganisthos*, also appear to be somewhat spiny (see Burmeister's figure of *A. Orion*, *loc. cit.* Pl. V. Fig. 6), and this raises the question as to whether the genus is correctly located in its present position. The larvæ of the following genera figured in Moore's "Lepidoptera of Ceylon," parts i. and ii., are all spiny: – 6, *Cirrochroa* (Pl. XXXII.); 7, *Cynthia* (Pl. XXVI.); 27, *Kallima* (Pl. XIX.); and 74, *Parthenos* (Pl. XXIV.). Many species of caterpillars which are spiny when adult appear to be spineless, or only slightly hairy when young. See Edwards' figures of *Melitæa Phaeton*, *Argynnis Diana*, and *Phyc. Tharos* (*loc. cit.*) and his description of the larva of *Arg. Cybele*, "Canad. Entom." vol. xii. p. 141. The spiny covering thus appears to be a character acquired at a comparatively recent period in the phyletic development. R.M.]

[10] [The larvæ of the 110th genus, *Paphia*, Fabr. (*Anæa*, Hübn.) are also smoothed-skinned. See Edwards' figure (*loc. cit.* vol. i. Pl. XLVI.) of *P. Glycerium*. Also C. V. Riley's "Second Annual Report" on the insects of Missouri, 1870, p. 125. Burmeister figures the larva of a species of *Prepona* (genus 99) which is smooth (*P. Demophon*, *loc. cit.* Pl. V. Fig. 1). The horns on the head of *Apatura*, &c., may possibly be a survival from a former spiny condition. R.M.]

from those of the latter sub-family in the absence of an enlargement of certain veins of the fore-wings, an essential character of the *Satyrinæ*.

This double disagreement has also been noticed by those systematists who have taken the form of the caterpillar into consideration. Thus, Morris[11] attempted to incorporate the genera *Apatura* and *Nymphalis* into the family *Libytheidæ*, placing the latter as transitional from the *Nymphalidæ* to the *Satyridæ*. But although the imagines of the genera *Apatura*, *Nymphalis*, and *Libythea* may be most closely related – as I believe they actually are – the larvæ are widely different, being at least as different as are those of *Apatura* and *Nymphalis* from the remaining *Nymphalinæ*.

Now if we could safely raise *Apatura* and *Nymphalis* into a distinct family – an arrangement which in the estimation of Staudinger[12] is correct – and if this were interpolated between the *Satyridæ* and *Nymphalidæ*, such an arrangement could only be based on the larval structure, and that of the imagines would thus remain unconsidered, since no other common characters can be found for these two genera than those which they possess in common with the other Nymphalideous genera.

The emperor-butterflies (*Apatura*), by the ocelli of their fore-wings certainly put us somewhat in mind of the *Satyrinæ*, in which such spots are always present; but this character does not occur in the genus *Nymphalis*, and is likewise absent in most of the other genera of this group. The genus *Apatura* shows in addition a most striking similarity in the markings of the wings to the purely Nymphalideous genus *Limenitis*, and it is therefore placed, by those systematists who leave this genus in the same family, in the closest proximity to *Limenitis*. This resemblance cannot depend upon mimicry, since not only one or another but *all* the species of the two genera possess a similar marking; and further, because similarity of marking alone does not constitute mimicry, but a resemblance in colour must also be added. The genus *Limenitis* actually contains a case of imitation, but in quite another direction; this will be treated of subsequently.

It cannot therefore be well denied that in this case the larvæ show different relationships to the imagines.

If the "natural" system is the expression of the genetic relationship of living forms, the question arises in this and in similar cases as to whether the more credence is to be attached to the larvæ or to the imagines – or, in more scientific phraseology, which of the two inherited classes of characters have been the most distinctly and completely preserved, and which of these, through its form-relationship, admits of the most distinct recognition of the blood-relationship, or, inversely, which has diverged the most widely from the ancestral form? The decision in single instances cannot but be difficult, and appears indeed at first sight impossible; nevertheless this will be arrived at in most cases as soon as the ontogeny of the larvæ, and therewith a portion of the phylogeny of this stage, can be accurately ascertained.

As in the *Rhopalocera* most of the families show a complete congruence in the form-relationship of the caterpillars and perfect insects, so a similar congruence is also found in the majority of the families belonging to other groups. Thus, the two allied families of the group *Sphingina* can also be very well characterized by their larvæ;[13] both the *Sphingidæ* and the *Sesiidæ* possess throughout a characteristic form of larva.

Of the group *Bombycina* the family of the *Saturniidæ* possess thick cylindrical caterpillars, of which the segments are beset with a certain number of knob-like warts. It is true that two genera of this family (*Endromis* and *Aglia*) are without these characteristic warts, but the imagines of these genera also show extensive and common differences from those of the other genera. A distinct family

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[11] "Synopsis of the described Lepidoptera of North America." Washington, 1862.

[12] "Catalog der Lepidopteren des Europäischen Faunengebietes." Dresden, 1871.

[13] This group of moths ("Schwärmer") is regarded as of very different extents by systematists; when I here comprise under it only the *Sphingidæ* proper and the *Sesiidæ*, I by no means ignore the grounds which favour a greater extension of the group; the latter is not rigidly limited. [The affinities of the *Sesiidæ* (*Ægeriidæ*) are by no means clearly made out: it appears probable that they are not related to the *Sphingidæ*. See note 160, p. 370. R.M.]

has in fact already been based on these genera (*Endromidæ*, Boisd.). Thus the congruence is not thereby disturbed.

So also the families *Liparidæ*, *Euprepiidæ*, and *Lithosiidæ* appear sharply defined in both forms; and similar families occur likewise under the *Noctuina*, although in this group the erection of families presents great difficulties owing to the near relationship of the genera, and is always to some extent arbitrary. It is important, however, that it is precisely the transitional families which present intermediate forms both as larvæ and as imagines.

Such an instance is offered by the *Acronyctidæ*, a family belonging to the group *Noctuina*. The imagines here show in certain points an approximation to the group *Bombycina*; and their larvæ, which are thickly covered with hairs, likewise possess the characteristics of many of the caterpillars of this group.[14]

A second illustration is furnished by the family *Ophiusidæ*, which is still placed by all systematists under the *Noctuina*, its affinity to the *Geometrina*, however, being represented by its being located at the end of the *Noctuina*. The broad wings and narrow bodies of these moths remind us in fact of the appearance of the "geometers;" and the larvæ, like the imagines, show a striking resemblance to those of the *Geometrina* in the absence of the anterior abdominal legs. For this reason Hübner in his work on caterpillars has termed the species of this family "*Semi-Geometræ*."

All these cases show a complete congruence in the two kinds of form-relationship; but exceptions are not wanting. Thus, the family *Bombycidæ* would certainly never have been formed if the larval structure only had been taken into consideration, since, whilst the genera *Gastropacha*, *Clisiocampa*, *Lasiocampa*, *Odonestis*, and their allies, are thickly covered with short silky hairs disposed in a very characteristic manner, the caterpillars of the genus *Bombyx*, to which the common silkworm, *B. Mori*, belongs, are quite naked and similar to many Sphinx-caterpillars (*Chærocampa*). Are the imagines of the genera united under this family, at any rate morphologically, as unequally related as their larvæ? Whether it is correct to combine them into one family is a question that does not belong here; we are now only concerned with the fact that the two stages are related in form in very different degrees.

An especially striking case of incongruence is offered by the family *Notodontidæ*, under which Boisduval, depending only on imaginal characters, united genera of which the larvæ differed to a very great extent. In O. Wilde's work on caterpillars this family is on this account quite correctly characterized as follows: – "Larvæ of various forms, naked or with thin hairs, sixteen or fourteen legs."[15] In fact in the whole order Lepidoptera there can scarcely be found associated together such diverse larvæ as are here placed in one imago-family; on one side the short cylindrical caterpillars of the genus *Cnethocampa*, Steph. (*C. Processionea*, *Pithyocampa*, &c.), which are covered with fine, brittle, hooked hairs, and are very similar to the larvæ of *Gastropacha* with which they were formerly united; and on the other side there are the naked, humped, and flat-headed larvæ of the genus *Harpyia*, Ochs., with their two long forked appendages replacing the hindmost pair of legs, and the grotesquely formed caterpillars of the genera *Stauropus*, Germ., *Hybocampa*, Linn., and *Notodonta*, Ochs.

The morphological congruence between larvæ and imagines declares itself most sharply in genera, where it is the rule almost without exception. In this case we can indeed be sure that a genus or sub-genus founded on the imagines only will, in accordance with correct principles, present a corresponding difference in the larvæ. Had the latter been known first we should have been led

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[14] [For Mr. A. G. Butler's observations on the genus *Acronycta*, see "Trans. Ent. Soc." 1879, p. 313; and note 68, p. 169, of the present volume. R.M.]

[15] [The following characters are given in Stainton's "Manual of British Butterflies and Moths," vol. i. p. 114: – "Larva of very variable form: at one extreme we find the singular *Cerura* larvæ, with only fourteen legs, and two long projecting tails from the last segment; at the other extreme we have larvæ with sixteen legs and no peculiarity of form, such as *Chaonia* and *Bucephala*; most have, however, the peculiarity of holding the hind segment of the body erect when in repose; generally quite naked, though downy in *Bucephala* and rather hairy in *Curtulu*; very frequently there are projections on the back of the twelfth segment." R.M.]

to construct the same genera as those which are now established on the structure of the imagines, and these, through other circumstances, would have stood in the same degree of morphological relationship as the genera founded on the imagines. There is therefore a congruence in a double sense; in the first place the differences between the larvæ and imagines of any two genera are equally great, and, in the next place, the common characters possessed by these two stages combined cause them to form precisely the same groups defined with equal sharpness; the genera coincide completely.

So also the butterflies of the sub-family *Nymphalinæ* can well be separated into genera by the characters of the larvæ, and these, as far as I am able to judge, would agree with the genera founded on the imagines.

The genus *Melitæa*, for example, can be characterized by the possession of 7–9 fleshy tubercles bearing hairy spines; the genus *Argynnis* may be distinguished by always having six hairy unbranched spines on each segment, and the genus *Cethosia* by two similar spines on each segment; the genus *Vanessa* shows sometimes as many as seven branched spines; and the genus *Limenitis* never more than two branched blunt spines on each segment, and so forth. If we go further into details it will be seen that the most closely related imagines, as might indeed have been expected, likewise possess the most nearly allied larvæ, whilst very small differences between the imagines are also generally represented by corresponding differences in the larvæ. Thus, for instance, the genus *Vanessa* of Fabricius has been divided into several genera by later authors. Of these sub-genera, *Grapta*, Doubl. (containing the European *C. – album*, the American *Fabricii*, *Interrogationis*, *Faunus*, *Comma*, &c.), is distinguished by the fact that the larvæ not only possess branched spines on all the segments with the exception of the prothorax, but these spines are also present on the head; in the genus *Vanessa* (*sensû strictiori*), Doubl., the head and prothorax are spineless (*e. g. V. Urticæ*); in the tropical genus *Junonia*, Hübn., which was also formerly (Godart, 1819[16]) united with *Vanessa*, the larvæ bear branched spines on all the segments, the head and prothorax included.

It is possible to go still further and to separate two species of *Vanessa* as two new genera, although they have hitherto been preserved from this fate even by the systematists most given to "splitting." This decision is certainly justifiable, simply because these species at present stand quite alone, and the practical necessity of forming a distinct genus does not make itself felt, and this practical necessity moreover frequently comes into conflict with scientific claims: science erects a new genus based on the amount of morphological difference, it being quite immaterial whether one or many species make up this genus; such an excessive subdivision is, however, a hindrance to practical requirements, as the cumbrous array of names thereby becomes still further augmented.

The two species which I might separate from *Vanessa* on the ground of their greater divergence, are the very common and widely distributed *V. Io* and *Antiopa*, the Peacock Butterfly and the Camberwell Beauty. In the very remarkable pattern of their wings, both show most marked characteristics; *Io* possesses a large ocellus on each wing, and *Antiopa* has a broad light yellow border which is not found in any other species of *Vanessa*. There can be no doubt but that each of these would have been long ago raised into a genus if similarly marked species of *Vanessa* occurred in other parts of the world, as is the case with the other species of the genus. Thus, it is well known that there is a whole series of species resembling our *V. Cardui*, and another series resembling our *V. C. – album*, the two series possessing the same respective types of marking; indeed on these grounds the sub-genera *Pyrameis* and *Grapta* have been erected.[17]

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[16] Encyl. Meth. ix. p. 310.

[17] [The genus *Vanessa* (in the wide sense) appears to be in a remarkable condition of what may be called phyletic preservation. Thus, the group of species allied to *V. C. – album* passes by almost insensible steps into the group of butterflies typified by our "Tortoiseshells." The following is a list of some of the intermediate species in their transitional order: —*I. – album*, *V. – album*, *Faunus*, *Comma*, *California*, *Dryas*, *Polychloros*, *Xanthomelas*, *Cashmirensis*, *Urticæ*, *Milberti*, &c. Similarly, our *Atalanta* and *Cardui* are connected by a number of intermediate forms, showing a complete transition from the one to the other. The following is the order of the species so far as I am acquainted with them: —*Atalanta*, *Dejeanii*, *Callirhoë*, *Tammeamea*, *Myrinna*, *Huntera*, *Terpsichore*, *Carye*, *Kershawii*, and *Cardui*. R.M.]

I should not have considered it worth while to have made these remarks if it had not been for the fact that the caterpillars of *V. Io* and *V. Antiopa* differ in small particulars from one another and from the other species of the genus. These differences relate to the number and position of the spines, as can be seen from the following table: —

Species of the Genus Vanessa, Fabr.

	Number of Spines on the head and segments of the larva.							
	Head.	Segm. I.	Segm. II.	Segm. III.	Segm. IV.	Segm. V.	Segm. VI.–XI.	Segm. XII.
V. Io	0	0	2	2	4	6	6	4
V. Antiopa	0	0	4	4	6	6	7	4
V. Urticæ	0	0	4	4	7	7	7	4
V. Polychloros	0	0	4	4	7	7	7	4
V. Ichnusa	0	0	4	4	7	7	7	4
V. Atalanta	0	0	4	4	7	7	7	4
V. C. — album	2	0	4	4	7	7	7	4
V. Interrogationis	2	0	4	4	7	7	7	4
V. Levana	2	0	4	4	7	7	7	4

This character of the number of spines will not be considered as too unimportant when we observe how perfectly constant it remains in the nearly allied species. This is the case in the three consecutive forms, *Urticæ*, *Polychloros*, and *Ichnusa*. Now when we see that two species which differ in their imaginal characters present correspondingly small differences in their larvæ, this exact systematic congruence indicates a completely parallel phyletic development.

Exceptions are, however, to be met with here. Thus, Hübner has united one group of the species of *Vanessa* into the genus *Pyrameis* just mentioned, on account of certain characteristic distinctions of the butterflies. I do not know, however, how this genus admits of being grounded on the structure of the larvæ; the latter, as appears from the above table, agree exactly in the number and position of the spines with the caterpillars of *Vanessa* (*sensû strictiori*), nor can any common form of marking be detected which would enable them to be separated from *Vanessa*.

Still more striking is the incongruence in the genus *Araschnia*, Hübn. (*A. Prorsa-Levana*), which, like the genus *Pyrameis*, is entirely based on imaginal characters. This is distinguished from all the other sub-genera of the old genus *Vanessa* by a small difference in the venation of the wings (the discoidal cell of the hind-wings is open instead of closed). Now it is well-known that in butterflies the wing-venation, as most correctly shown by Herrich-Schäffer, is the safest criterion of "relationship." It thus happens that this genus, typified by the common *Levana*, is in Kirby's Catalogue separated from *Vanessa* by two genera, and according to Herrich-Schäffer[18] by forty genera! Nevertheless, the larvæ agree so exactly in their spinal formula with *Grapta* that we should have no hesitation in regarding them as a species of this sub-genus. It appears to me very probable that in this case the form-relationship of the caterpillar gives more correct information as to the blood-relationship of the species than that of the imago – in any case the larvæ show a different form-relationship to the imagines.

Just as in the case of butterflies there are many genera of *Sphingidæ* which can be based on the structure of the larvæ, and which agree with those founded on the imagines.

Thus, the genus *Macroglossa* is characterized by a straight anal horn, a spherical head, and by a marking composed of longitudinal stripes, these characters not occurring elsewhere in this combination. The nearly allied genus *Pterogon*, on the other hand, cannot be based on the larvæ only, since not only is the marking of the adult larva very distinct in the different species, but the anal horn is present in two species, whilst in a third (*P. Œnotheræ*) it is replaced by a knob-like eye-spot.

[18] "Prodromus Systematis Lepidopterorum." Regensburg, 1864.

The genus *Sphinx* (*sensû strictiori*) is distinguished by the simple, curved caudal horn, the smooth, egg-shaped head and smooth skin, and by a marking mainly composed of seven oblique stripes. The genus *Deilephila* is distinguished from the preceding by a dorsal plate, situated on the prothorax and interrupting the marking, as well as by the pattern, which here consists of a subdorsal line with ring-spots more or less numerous and developed; the skin also is rough, "shagreened," although it must be admitted that there are exceptions (*Vespertilio*). The genus *Chœrocampa* admits also of being based on the form-relationship of its caterpillars, although this is certainly only possible by disregarding the marking and taking alone into consideration the peculiar pig-like form of the larvæ. The genus *Acherontia*, so nearly related to *Sphinx*, possesses in the doubly curved caudal horn a character common to the genus (three species known[19]). Finally may be mentioned the genus *Smerinthus*, of which the larvæ, by their anteriorly tapering form, their shagreened skin and almost triangular head with the apex upwards, their simply curved anal horn, and by their seven oblique stripes on each side, constitute a genus as sharply defined as that formed by the moths.

Although in all the systematic divisions hitherto treated of there are cases where the form-relationship of the larva does not completely coincide with that of the imago, such incongruences are of far more frequent occurrence in the smallest systematic group, viz. species.

The larvæ of two species have very frequently a much nearer form-relationship than their imagines. Thus, the caterpillars of *Smerinthus Ocellatus* and *S. Populi* are closely allied in structure, marking, and colouring, whilst the moths in these two last characters and in the form of the wings are widely separated.[20] Judging from the larvæ we should expect to obtain two very similar moths, but in fact both *Populi* and *Ocellatus* have many near allies, and these closely related species sometimes possess larvæ which differ more widely than those of more distantly related species of imagines.

Thus, in Amur-land and North America there occur species of *Smerinthus* which closely resemble our *Ocellatus* in colour, marking, and form of wing, and which possess the characteristic large blue ocellus on the hind-wings. *S. Excæcatus* is quite correctly regarded as the representative American form of our *Ocellatus*, but its caterpillar, instead of being leaf-green, is of a chrome-yellow, and possesses dark green instead of white oblique stripes, and has moreover a number of red spots, and a red band on the head – in brief, in the very characters (colour and certain of the markings) in which the imagines completely agree it is widely different from *Ocellatus*. It appears also to be covered with short bristles, judging from Abbot and Smith's figure.[21]

Just in the same way that the species having the nearest conceivable form-relationship to *Ocellatus* possesses a relatively strongly diverging larva, so does the nearest form-relation of *Populi* (imago) offer a parallel case. This species, which is also North American, lives on *Juglans Alba*. The imago of *Smerinthus Juglandis* differs considerably from *S. Populi* in the form of the wings, but it resembles the European species so closely in marking and colouring that no doubt can exist as to the near relationship of the two forms. The caterpillar of *S. Juglandis*,[22] however, differs to a great extent from that of *Populi* in colour – it is not possible to confound these two larvæ; but those of *Populi* and *Ocellatus* are not only easily mistaken for one another, but are distinguished with difficulty even by experts.

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[19] [The larva of *Acherontia Morta*, figured by Butler (see note 121, p. 262), possesses the characteristically recurved horn; that of *Ach. Medusa* figured by the same author, does not appear to possess this character in any marked degree. R.M.]

[20] [See note 97, p. 233. R.M.]

[21] *Loc. cit.* Pl. XXV. [This species is referred by Butler to the genus *Paonias*, Hübn. R.M.]

[22] Abbot and Smith, Pl. XXIX. [Placed by Butler in the genus *Cressonia*, Grote and Robinson. Abbot and Smith state that this larva is sometimes green. According to Mr. Herman Strecker (Lepidop. Rhopal. and Hetero, Reading, Pa. 1874, p. 54) it feeds upon black walnut (*Juglans Nigra*), hickory (*Carya Alba*), and ironwood (*Ostrya Virginica*). Of the North American species of *Smerinthus*, the following, in addition to *Excæcatus*, closely resemble our *Ocellatus*: —*S. (Calasymbolus) Geminatus*, Say; *(C.) Cerisii*, Kirby; and *Ophthalmicus*, Boisd. In addition to *S. (Cressonia) Juglandis*, *S. (Triptogon) Modesta* much resembles our *Populi*. The larva of *Geminatus*, according to Strecker, is "pale green, lightest above, with yellow lateral granulated stripes; caudal horn violet; stigmata red. It feeds on the willow." R.M.]

In this same family of the *Sphingidæ* cases are not wanting in which, on the other hand, the moths are far more closely allied than the larvæ. This is especially striking in the genus *Deilephila*, eight species of which are allied in the imaginal state in a remarkable degree, whilst the larvæ differ greatly from one another in colour, and to as great an extent in marking. These eight species are *D. Nicæa*, *Euphorbiæ*, *Dahlii*, *Galii*, *Livornica*, *Lineata*, *Zygophylli*, and *Hippophaës*. Of these, *Nicæa*, *Euphorbiæ*, *Dahlii*, *Zygophylli*, and *Hippophaës* are so much alike in their whole structure, in the form of the wings, and in marking, that few entomologists can correctly identify them off-hand without comparison. The larvæ of these four species, however, are of very different appearances. Those of *Euphorbiæ* and *Dahlii* are most alike, both being distinguished by the possession of a double row of large ring-spots. *Zygophylli* (see Fig. 50, Pl. VI.) possesses only faint indications of ring-spots on a white subdorsal line; and in *Hippophaës* there is only an orange-red spot on the eleventh segment, the entire marking consisting of a subdorsal line on which, in some individuals, there are situated more or less developed ring-spots (see Figs. 59 and 60, Pl. VII.). If we only compare the larvæ and imagines of *D. Euphorbiæ* and *Hippophaës*, we cannot but be struck with astonishment at the great difference of form-relationship in the two stages of development.

In the case of *D. Euphorbiæ* and *Nicæa* this difference is almost greater. Whilst these larvæ show great differences in colour, marking, and in the roughness or smoothness of the skin (compare Fig. 51, Pl. VI. with Figs. 43 and 44, Pl. V.), the moths cannot be distinguished with certainty. As has already been stated, the imago of the rare *D. Nicæa* is for this reason wanting in most collections; it cannot be detected whether a specimen is genuine, *i. e.* whether it may not perhaps be a somewhat large example of *D. Euphorbiæ*.

An especially striking instance of incongruence is offered by the two species of *Chærocampa* most common with us, viz., *Elpenor* and *Porcellus*, the large and small Elephant Hawk-moths. The larvæ are so similar, even in the smallest details of marking, that they could scarcely be identified with certainty were it not that one species (*Elpenor*) is considerably larger and possesses a less curved caudal horn than the other. The moths of these two species much resemble one another in their dull green and red colours, but differ in the arrangement of these colours, *i. e.* in marking, and also in the form of their wings, to such an extent that *Porcellus* has been referred to the genus *Pergesa*[23] of Walker. If systemy, as is admitted on many sides, has only to indicate the morphological relationship, this author is not to blame – but in this case a special larval classification must likewise be admitted, in a manner somewhat similar to that at present adopted provisionally in text-books of zoology for the Hydroid Polypes and inferior Medusæ. This case of *Porcellus*, however, shows that those are correct who maintain that systemy claims to express, although incompletely, the blood-relationship, and that systematists have always unconsciously formed their groups as though they intended to express the genetic connection of the forms. Only on this supposition can it appear incorrect to us to thus separate two species of which the larvæ agree so completely.

I cannot conclude this review of the various systematic groups without taking a glance at the groups comprised within species, viz. varieties. Whilst in species incongruence is of frequent occurrence, in varieties this is the rule, for which reason it admits in this case of being more sharply defined, since we are not concerned with a double difference but only with the question whether in the one stage a difference or an absolute similarity is observable. By far the majority of varieties are either simply imaginal or merely larval varieties – only the one stage diverges, the other is quite constant.

Thus, as has already been shown, in all the seasonally dimorphic butterflies known to me the caterpillars of the two generations of imagines, which are often so widely different, are exactly alike; and the same obtains for the majority of purely climatic varieties of butterflies. Unfortunately there are as yet no connected observations on this point. The only certain instance that I can here mention is that of the Alpine and Polar form of *Pteris Napi*. This variety, *Bryoniæ*, the female of which differs

[23] Cat. Brit. Mus.

so greatly in marking and colouring, possesses larvæ which cannot be distinguished from those of the ordinary form of *Napi*.(See part I. appendix I. p. 124.)

That caterpillars can also vary locally without thereby affecting the imagines is shown by the frequently mentioned and closely investigated cases of di- and polymorphism in the larvæ of a number of *Sphingidæ* (*M. Stellatarum*, *A. Atropos*, *S. Convolvuli*, *C. Elpenor*, and *Porcellus*, &c.). The same thing is still more clearly shown by those instances in which there are not several but only one distinct larval form occurring in each of two different localities.

To this class belongs the above-mentioned case of *Chærocampa Celerio* (p. 197), supposing our information concerning this species to be correct; likewise the recently-mentioned case of the Ligurian variety of the caterpillar of *Saturnia Carpini*; and finally the case of *Eriogaster Lanestris*, so well known to lepidopterists. This insect inhabits the plains of Germany, and in the Alps extends to an elevation of 7000 feet, where it possesses a larva differently marked and coloured (*E. Arbusculæ*) to those of the lowlands whilst the moths are smaller, but do not differ in other respects from those of the plains.

Among the Alpine species many other such cases may occur, but these could only be discovered by making investigations having special reference to this point. Of the Alpine butterflies, for example, not a single species can have been reared from the caterpillar; for this reason but few observations have on the whole been given by entomologists respecting the Alpine larvæ, which are not known sufficiently well to enable such a question to be decided.

The investigation of the form-relationships existing between larvæ on the one hand and imagines on the other has thus led to the following results: —

We learn on comparison that incongruences or inequalities of form-relationship occur in all systematic groups from varieties to families. These incongruences are of two kinds, in some cases being disclosed by the fact that the larvæ of two systematic groups, *e. g.* two species, are more closely related in form than their imagines (or inversely), whilst in other cases the larvæ form different systematic groups to those formed by the imagines.

The results of the investigation into the occurrence of incongruences among the various systematic groups may be thus briefly summarised: —

Incongruences appear to occur most frequently among varieties, since it very frequently happens that it is only the larva or only the imago which has diverged into a variety, the other stage remaining monomorphic. The systematic division of varieties is thus very often one-sided.

Among species also incongruences are of frequent occurrence. Sometimes the imagines are much more nearly related in form than the larvæ, and at others the reverse happens; whilst again the case appears also to occur in which only the one stage (larva) diverges to the extent of specific difference, the other stage remaining monomorphic (*D. Euphorbiæ* and *Nicæa*).

The agreement in form-relationship appears to be most complete in genera. In the greater number of cases the larval and imaginal genera coincide, not only in the sharpness of their limits, but also – as far as one can judge – in the weight of their distinctive characters, and therefore in the amount of their divergence. Of all the systematic groups, genera show the greatest congruence.

In families there is again an increase of irregularity. Although larval and imaginal families generally agree, there are so many exceptions that the groups would be smaller if they were based exclusively on the larval structure than if founded entirely on the imagines (*Nymphalidæ*, *Bombycidæ*).

If we turn to the groups of families we find a considerably increased incongruence; complete agreement is here again rather the exception, and it further happens in these cases that it is always the larvæ which, to a certain extent, remain at a lower grade, and which form well defined families; but these can seldom be associated into groups of a higher order having a common character, as in the case of the imagines (*Rhopalocera*).

After having thus collected (so far as I am able) the facts, we have now to attempt their interpretation, and from the observed congruence and incongruence of form-relationship of the two stages to endeavour to draw a conclusion as to the underlying causes of the transformations.

It is clear at starting that all cases of incongruence can only be the expression or the consequence of a phyletic development which has not been exactly parallel in the two stages of larva and imago – that one stage must have changed either more rapidly or more slowly than the other. An "unequal phyletic development" is thus the immediate cause of incongruence.

Thus, the occurrence of different larvæ in species of which the imagines have remained alike may be simply understood as cases in which the imago only has experienced a change – has taken a forward step in phyletic development, whilst the larvæ have remained behind. If we conceive this one-sided development to be repeated several times, there would arise two larval forms as widely different as those of *Deilephila Nicæa*, and *Euphorbiæ*, whilst the imagines, as is actually the case in these species, would remain the same.

The more commonly occurring case in which one stage has a greater form-divergence than the other, is explicable by the one stage having changed more frequently or more strongly than the other.

The explanation of the phenomena thus far lies on the surface, and it is scarcely possible to advance any other; but why should one stage become changed more frequently or to a greater extent than the other? why should one portion be induced to change more frequently or more strongly than another? whence come these inducements to change? These questions bring us to the main point of inquiry: – Are the causes which give rise to these changes internal or external? Are the latter the result of a phyletic vital force, or are they only due to the action of the external conditions of life?

Although an answer to this question will be found in the preceding essay, I will not support myself on the results there obtained, but will endeavour to give another solution of the problem on fresh grounds. The answer will indeed be the same as before: – A phyletic force must be discountenanced, since in the first place it does not explain the phenomena, and in the second place the phenomena can be well explained without its assumption.

The admission of a phyletic vital force does not explain the phenomena. The assumption that there is a transforming power innate in the organism indeed agrees quite well with the phenomenon of congruence, but not with that of incongruence. Since a large number of cases of the latter depend upon the fact that the larvæ are more frequently influenced by causes of change than their imagines, or *vice versâ*, how can this be reconciled with such an internal force? On this assumption would not each stage of a species be compelled to change, if not contemporaneously at least successively, with the same frequency and intensity, by the action of an innate force? and how by means of the latter can there ever result a greater form-divergence in the larvæ than in the imagines?

It is delusive to believe that these unequal deviations can be explained by assuming that the phyletic force acts periodically. Granting that it does so, and that the internal power successively compels the imago, pupa, and finally the larva to change, there would then pass a kind of wave of transformation over the different stages of the species, as was actually shown above to be the case in the single larval stages. The only possible way of explaining the unequal distances between larvæ and imagines would therefore be to assume that two allied groups, *e. g.* species, were not contemporaneously affected by the wave, so that at a certain period of time the imago alone of one species had become changed, whilst in the other species the wave of transformation had also reached the larva. In this case the imagines of the two species would thus appear to be more nearly related than their larvæ.

Now this strained explanation is eminently inapplicable to varieties, still less to species, and least of all to higher systematic groups, for the simple reason that every wave of transformation may be assumed to be at the most of such strength as to produce a deviation of form equal to that of a variety. Were the change resulting from a single disturbance greater, we should not only find one-sided varieties, *i. e.* those belonging to *one* stage, but we should also meet as frequently with one-sided species. If, however, a wave of transformation can only produce a variety even in the case of greatest form-divergence, the above hypothetical uncontemporaneous action of such a wave in two species could only give rise to such small differences in the two stages that we could but designate them as varieties. An accumulation of the results of the action of several successive waves passing over the same species could not happen, because the distance from a neighbouring species would always become the same in two stages as soon as *one* wave had ended its course. In this manner there could therefore only arise divergences of the value of varieties, and incongruences in systematic groups of a higher rank could not thus be explained.

All explanations of the second form of incongruence from the point of view of a phyletic force can also be shown to be absurd. How can the fact be explained that larval and imaginal families by no means always coincide; or that the larvæ can only be formed into families whilst the imagines partly form sharply defined groups of a higher order? How can an internal directive force within the same organism urge in two quite distinct directions? If the evolution of a definite system were designed, and the admission of such a continually acting power rendered necessary, why such an incomplete, uncertain, and confused performance?

I must leave others to answer these questions; to me a vital force appears to be inadmissible, not only because we cannot understand the phenomena by its aid, but above all because it is superfluous for their explanation. In accordance with general principles the assumption of an unknown force can, however, only be made when it is indispensable to the comprehension of the phenomena.

I believe that the phenomena can be quite well understood without any such assumption – both the phenomena of congruence and incongruence, in their two forms of unequal divergence and unequal group-formation.

Let us in the first place admit that there is no directive force in the organism inciting periodic change, but that every change is always the consequence of external conditions, being ultimately nothing but the reaction – the response of the organism to some of the influences proceeding from the environment; every living form would in this case remain constant so long as it was not compelled to change by inciting causes. Such transforming factors can act directly or indirectly, *i. e.* they can produce new changes immediately, or can bring about a remodelling by the combination, accumulation, or suppression of individual variations already present (adaptation by natural selection). Both forms of this action of external influences have long been shown to be in actual operation, so that no new assumption will be made, but only an attempt to explain the phenomena in question by the sole action of these known factors of species formation.

If, in the first instance, we fix our attention upon that form of incongruence which manifests itself through unequal divergence of form-relationship, it will appear prominently that this bears precise relations to the different systematic groups. This form of incongruence constitutes the rule in varieties of the order Lepidoptera, it is of very frequent occurrence in species, but disappears almost completely in genera, and entirely in the case of families and the higher groups. On the whole, therefore, as we turn to more and more comprehensive groups, the incongruence diminishes whilst the congruence increases, until finally the latter becomes the rule.

Now if congruence presupposes an equal number of transforming impulses, we perceive that the number of the impulses which have affected larvæ and imagines agree with one another the more closely the larger the systematic groups which are compared together. How can this be otherwise? The larger the systematic group the longer the period of time which must have been necessary for its formation, and the more numerous the transforming impulses which must have acted upon it before its formation was completed.

But if the supposition that the impulse to change always comes from the environment in no way favours the idea that such impulses always affect both stages contemporaneously, and are equal in number during the same period of time, there is not, on the other hand, the least ground for assuming that throughout long periods the larvæ or the imagines only would have been affected by such transforming influences. This could have been inferred from the fact that varieties frequently depend only upon one stage, whilst specific differences in larvæ only also occur occasionally, the imagines remaining alike; but no single genus is known of which all the species possess similar larvæ. Within the period of time during which genera can be formed the transforming impulses therefore never actually affect the one stage only, but always influence both.

But if this is the case – if within the period of time which is sufficient for the production of species, the one stage only is but seldom and quite exceptionally influenced by transforming impulses, whilst both stages are as a rule affected, although not with the same frequency, it must necessarily follow that on the whole, as the period of time increases, the difference in the number of these impulses which affect the larva and of those which affect the imago must continually decrease, and with this difference the magnitude of the morphological differences resulting from the transforming influences must at the same time also diminish. With the number of the successively increasing changes the difference in the magnitude of the change in the two stages would always relatively diminish until it had quite vanished from our perception; just in the same manner as we can distinguish a group of three grains of corn from one composed of six, but not a heap of 103 grains from one containing 106 grains.

That the small systematic groups must have required a short period and the large groups a long period of time for their formation requires no special proof, but results immediately from the theory of descent.

All the foregoing considerations would, however, only hold good if the transforming impulses were equal in strength, or, not to speak figuratively, if the changes only occurred in equivalent portions of the body, *i. e.* in such portions as those in which the changes are of the same physiological and morphological importance to the whole organism.

Now in the lower systematic groups this is always the case. Varieties, species, and genera are always distinguished by only relatively small differences; deep-seated distinctions do not here occur, as is implied in the conception of these categories. The true cause of this is, I believe, to be found in the circumstance that all changes take place only by the smallest steps, so that greater differences can only arise in the course of longer periods of time, within which a great number of types (species) can, however, come into existence, and these would be related by blood and in form in different degrees, and would therefore form a systematic group of a higher rank.

The short periods necessary for the production of inferior groups, such as genera, would not result in incongruences if only *un*typical parts of the larvæ, such as marking or spines, underwent change, whilst in the imagines typical parts – wings and legs – became transformed. The changes which could have occurred in the wings, &c., during this period of time would have been much too small to produce any considerable influence on the other parts of the body by correlation; and two species of which the larvæ and imagines, had changed with the same frequency, would show a similar amount of divergence between the larvæ and between the imagines, although on the one side only *un*typical parts —*i. e.* those of no importance to the whole organization – and on the other side typical parts, were affected. The *number* of the changes would here alone determine whether congruence or incongruence occurred between the two stages.

The case would be quite different if, throughout a long period of time, in the one stage only typical and in the other only untypical parts were subjected to change. In the first case a complete transformation of the whole structure would occur, since not only would the typical parts, such as the wings, undergo a much further and increasing transformation in the same direction, but these changes would also lead to secondary alterations.

In this manner, I believe, must be explained the fact that in the higher groups still greater form-divergences of the two stages occur; and if this explanation is correct, the cause of this striking phenomenon, viz., that incongruence diminishes from varieties to genera, in which latter it occurs but exceptionally, whilst in families and in the higher groups it again continually increases, is likewise revealed. Up to genera the incongruence depends entirely upon the one stage having become changed *more frequently* than the other; but in families and groups of families, and in the orders Diptera and Hymenoptera, as will be shown subsequently, in sub-orders and tribes, it depends upon the *importance of the part of the body* affected by the predominant change. In the latter case the number of changes is of no importance, because these are so numerous that the difference vanishes from our perception; but an equal number of changes, even when very great, may now produce a much greater or a much smaller transformation in the entire bodily structure according as they affect typical or untypical portions, or according as they keep in the same direction throughout a long period of time, or change their direction frequently.

Those unequal form-divergences which occur in the higher systematic groups a re always associated with a different formation of groups – the larvæ form different systematic groups to the imagines, so that one of these stages constitutes a higher or a lower group; or else the groups are of equal importance in the two stages, but are of unequal magnitude – they do not coincide, but the one overlaps the other.

Incongruences of this last kind appear in certain cases within families (*Nymphalidæ*), but I will not now subject these to closer analysis, because their causes will appear more clearly when subsequently considering the orders Hymenoptera and Diptera. Incongruences of the first kind, however, admit of a clear explanation in the case of butterflies. They appear most distinctly in the groups composed of families.

Nobody has as yet been able to establish the group *Rhopalocera* by means of any single character common to the larvæ; nevertheless, this group in the imagines is the sharpest and best defined of the whole order. If we inform the merest tyro that clubbed antennæ are the chief character of the butterflies, he will never hesitate in assigning one of these insects to its correct group. Such a typical character, common to all families, is, however, absent in the larvæ; and it might be correctly said that there were no Rhopalocerous larvæ, or rather that there were only larvæ of *Equites*, *Nymphales*, and *Heliconii*. The larvæ of the various families can be readily separated by means of characteristic distinctions, and it would not be difficult for an adept to distinguish to this extent in single cases a Rhopalocerous caterpillar as such; but these larvæ possess only *family* characters, and not those of a higher order.

This incongruence partly depends upon the circumstance that the form-divergence between a Rhopalocerous and a Heterocerous family is much greater on the side of the imagines than on that of the larvæ. Were there but a single family of butterflies in existence, such as the *Equites*, we should be obliged to elevate this to the rank of a sub-order on the side of the imagines, but not on that of the larvæ. Such cases actually occur, and an instance of this kind will be mentioned later in connection with the Diptera. But this alone does not explain why, on the side of the imagines, a whole series of families show the same amount of morphological divergence from the families of other groups. There are two things, therefore, which must here be explained: – First, why is the form-divergence between the imagines of the Rhopalocera and Heterocera greater than that between their larvæ? and, secondly, why can the imagines of the Rhopalocera be formed into one large group by means of common characters whilst the larvæ cannot?

The answers to both these questions can easily be given from our present standpoint. As far as the first question is concerned, this finds its solution in the fact that the form-divergence always corresponds exactly with the divergence of function, *i. e.* with the divergence in the mode of life.

If we compare a butterfly with a moth there can be no doubt that the difference in the conditions of life is far greater on the side of the imagines than on that of the larvæ. The differences in the mode of life of the larvæ are on the whole but very small. They are all vegetable feeders, requiring large quantities of food, and can only cease feeding during a short time, for which reason they never leave their food-plants for long, and it is of more importance for them to remain firmly attached than to be able to run rapidly. It is unnecessary for them to seek long for their food, as they generally find themselves amidst an abundance, and upon this depends the small development of their eyes and other organs of sense. On the whole caterpillars live under very uniform conditions, although these may vary in manifold details.

The greatest difference in the mode of life which occurs amongst Lepidopterous larvæ is shown by wood feeders. But even these, which by their constant exclusion from light, the hardness of their food, their confinement within narrow hard-walled galleries, and by the peculiar kind of movement necessitated by these galleries, are so differently situated in many particulars to those larvæ which live openly on plants, have not experienced any general change in the typical conformation of the body by adaptation to these conditions of life. These larvæ, which, as has already been mentioned, belong to the most diverse families, are more or less colourless and flattened, and have very strong jaws and small feet; but in none of them do we find a smaller number of segments, or any disappearance, or important transformation of the typical limbs; they all without exception possess sixteen legs, like the other larvæ excepting the *Geometræ*.

Now if even under the most widely diverging conditions of life adaptation of form is produced by relatively small, and to a certain extent superficial, changes, we should expect less typical transformations in the great majority of caterpillars which live on the exterior of plants or in their softer parts (most of the Micro-lepidoptera). The great diversity in the forms of caterpillars depends essentially upon a different formation of the skin and its underlying portions. The skin is sometimes naked, and can then acquire the most diverse colours, either protective or conspicuous, or it may develop offensive or defensive markings; in other cases it may be covered with hairs which sting, or with spines which prick; certain of its glands may develop to an enormous size, and acquire brilliant colours and the power of emitting stinking secretions (the tentacles of the *Papilionidæ* and Cuspidate larvæ); by the development of warts, angles, humps, &c., any species of caterpillar may be invested with the most grotesque shape, the significance of which with respect to the life of the insect is as yet in most cases by no means clear: *typical portions* are not, however, essentially influenced by these manifold variations. At most only the form of the individual segments of the body, and with these the shape of the whole insect, become changed (onisciform larvæ of *Lycænidæ*), but a segment is never suppressed, and even any considerable lengthening of the legs occurs but very seldom (*Stauropus Fagi*).[24]

We may therefore fairly assert that the structure of larvæ is on the whole remarkably uniform, in consequence of the uniformity in the conditions of life. Notwithstanding the great variety of external aspects, the general structure of caterpillars does not become changed – it is only their outward garb which varies, sometimes in one direction, and sometimes in another, and which, starting from inherited characters, becomes adapted to the various special conditions of life in the best possible manner.

All this is quite different in the case of the imagines, where we meet with very important differences in the conditions of life. The butterflies, which live under the influence of direct sunlight and a much higher temperature, and which are on the wing for a much longer period during the day, must evidently be differently equipped to the moths in their motor organs (wings), degree of hairiness, and in the development of their eyes and other organs of sense. It is true that we are not at present in a condition to furnish special proofs that the individual organs of butterflies are exactly adapted to a diurnal life, but we may safely draw this general conclusion from the circumstance that no butterfly is of nocturnal habits.[25] It cannot be stated in objection that there are many moths which fly by day. It

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[24] [This lengthening of the true legs is mimetic according to Hermann Müller, and causes the anterior portion of the caterpillar to resemble a spider. See note 129, p. 290. R.M.]

[25] [Certain butterflies appear to be crepuscular, if not nocturnal in their habits. Thus in his "Notes on the Lepidoptera of Natal," Mr. W. D. Gooch states that he never saw *Melanitis*, *Leda*, or *Gnophodes Parmeno* on the wing by day, but generally during the hour after sunset. He adds: – "My sugar always attracted them freely, even up to 10 or 11 p.m." Many species of *Hesperidæ* are also stated to be of crepuscular habits by this same observer. See "Entomologist," vol xvi. pp. 38 and 40. R.M.]

certainly appears that no great structural change is necessary to confer upon a Lepidopteron organized for nocturnal life the power of also flying by day; but this proves nothing against the view that the structure of the butterflies depends upon adaptation to a diurnal life. Analogous cases are known to occur in many other groups of animals. Thus, the decapodous Crustacea are obviously organized for an aquatic life; but there are some crabs which take long journeys by land. Fish appear no less to be exclusively adapted to live in water; nevertheless the "climbing-perch" (*Anabas*) can live for hours on land.

It is not the circumstance that some of the moths fly by day which is extraordinary and demands a special explanation, but the reverse fact just mentioned, that no known butterfly flies by night. We may conclude from this that the organization of the latter is not adapted to a nocturnal life.

If we assume[26] that the Lepidopterous family adapted to a diurnal life gives rise in the course of time to a nocturnal family, there can be no doubt but that the transformation of structure would be far greater on the part of the imagines than on that of the larvæ. The latter would not remain quite unchanged – not because their imagines had taken to a nocturnal life which for the larva would be quite immaterial, but because this change could only occur very gradually in the course of a large number of generations, and during this long period the conditions of life would necessarily often change with respect to the larvæ. It has been shown above that within the period of time necessary for the formation of a new species impulses to change occur on both sides; how much more numerous therefore must these be in the case of a group of much higher rank, for the establishment of which a considerably longer period is required. In the case assumed, therefore, the larvæ would also change, but they would suffer much smaller transformations than the imagines. Whilst in the latter almost all the typical portions of the body would undergo deep changes in consequence of the entirely different conditions of life, the larvæ would perhaps only change in marking, hairs, bristles, or other external characters, the typical parts experiencing only unimportant modifications.

In this manner it can easily be understood why the larvæ of a family of *Noctuæ* do not differ to a greater extent from those of a family of butterflies than do the latter from some other Rhopalocerous family, or why the imagines of a Rhopalocerous and a Heterocerous family present much greater form-divergences than their larvæ. At the same time is therefore explained the unequal value that must be attributed to any single family of butterflies in its larvæ and in its imagines. The unequal form-divergences coincide exactly with the inequalities in the conditions of life.

When whole families of butterflies show the same structure in their typical parts (antennæ, wings, &c.), and, what is of more importance, can be separated as a systematic group of a higher order (*i. e.* as a section or sub-order) from the other Lepidoptera whilst their larval families do not appear to be connected by any common character, the cause of this incongruence lies simply in the circumstance that the imagines live under some peculiar conditions which are common to them all, but which do not recur in other Lepidopterous groups. Their larvæ live in precisely the same manner as those of all the other families of Lepidoptera – they do not differ in their mode of life from those of the Heterocerous families to a greater extent than they do from one another.

We therefore see here a community of form within the same compass as that in which there is community in the conditions of life. In all butterflies such community is found in their diurnal habits, and in accordance with this we find that these only, and not their larvæ, can be formed into a group having common characters.

In the larvæ also we only find agreement in the conditions of life within a much wider compass, viz. within the whole order. Between the limits of the order Lepidoptera the conditions of life in the caterpillars are, as has just been shown, on the whole very uniform, and the structure of the larvæ accordingly agrees almost exactly in all Lepidopterous families in every essential, *i. e.* typical, part.

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[26] I only make this assumption for the sake of simplicity, and not because I am convinced that the existing *Rhopalocera* are actually the oldest Lepidopterous group.

In this way is explained the hitherto incomprehensible phenomenon that the sub-ordinal group *Rhopalocera* cannot be based on the larvæ, but that Lepidopterous caterpillars can as a whole be associated into a higher group (order); they constitute altogether families and an order, but not the intermediate group of a sub-order. By this means we at the same time reply to an objection that may be raised, viz. that larval forms cannot be formed into high systematic groups because of their "low and undeveloped" organization.

To this form of incongruence, viz. to the formation of systematic groups of unequal value and magnitude, I must attach the greatest weight with respect to theoretical considerations. I maintain that this, as I have already briefly indicated above, is wholly incompatible with the admission of a phyletic force. How is it conceivable that such a power could work in the same organism in two entirely different directions – that it should in the same species lead to the constitution of quite different systems for the larvæ and for the imagines, or that it should lead only to the formation of families in the larvæ and to sub-orders in the imagines? If an internal force existed which had a tendency to call into existence certain groups of animal forms of such a nature that these constituted one harmonious whole of which the components bore to one another fixed morphological relationships, it would certainly have been an easy matter for such a power to have given to the larvæ of butterflies some small character which would have distinguished them as such, and which would in some measure have impressed them with the stamp of "*Rhopalocera*." Of such a character we find no trace however; on the contrary, everything goes to show that the transformations of the organic world result entirely from external influences.

III. Incongruences in other Orders of Insects

Although the order Lepidoptera is for many reasons especially favourable for an investigation such as that undertaken in the previous section, it will nevertheless be advantageous to inquire into the form-relationships of the two chief stages in some other orders of metamorphic insects, and to investigate whether in these cases the formation of systematic groups also coincides with common conditions of life.

Hymenoptera

In this order there cannot be the least doubt as to the form-relationship of the imagines. The characteristic combination of the pro- and meso-thorax, the number and venation of the wings, and the mouth-organs formed for biting and licking, are found throughout the whole order, and leave no doubt that the Hymenoptera are well based on their imaginal characters.

But it is quite different with the larvæ. It may be boldly asserted that the order would never have been founded if the larvæ only had been known. Two distinct larval types here occur, the one – caterpillar-like – possessing a distinct horny head provided with the typical masticatory organs of insects, and a body having thirteen segments, to which, in addition to a variable number of abdominal legs, there are always attached three pairs of horny thoracic legs: the other type is maggot-shaped, without the horny head, and is entirely destitute of mouth-organs, or at least of the three pairs of typical insect jaws, and is also without abdominal and thoracic legs. The number of segments is extremely variable; the larvæ of the saw-flies have thirteen besides the head, the maggot-shaped larvæ of bees possess fourteen segments altogether, and the gall-flies and ichneumons only twelve or ten. We should be much mistaken also if we expected to find connecting characters in the internal organs. The intestine is quite different in the two types of larvæ, the posterior opening being absent in the maggot-like grubs; at most only the tracheal and nervous systems show a certain agreement, but this is not complete.

The order Hymenoptera, precisely speaking and conceived only morphologically, exists therefore but in the imagines; in the larvæ there exist only the caterpillar- and maggot-formed groups. The former shows a great resemblance to Lepidopterous larvæ, and in the absence of all knowledge of the further development it might be attempted to unite them with these into one group. The two certainly differ in certain details of structure in the mouth-organs and in the number of segments, abdominal legs, &c., to a sufficient extent to warrant their being considered as two sub-orders of one larval order; but they would in any case be regarded as much more nearly related in form than the caterpillar- and maggot-like types of the Hymenopterous larvæ.

Is it not conceivable, however, that the imagines of the Hymenoptera – that ichneumons and wasps may be only accidentally alike, and that they have in fact arisen from quite distinct ancestral forms, the one having proceeded with the Lepidopterous caterpillars from one root, and the other with the grub-like Dipterous larvæ from another root?

This is certainly not the case; the common characters are too deep-seated to allow the supposition that the resemblance is here only superficial. From the structure of the imagines alone the common origin of all the Hymenoptera may be inferred with great probability. This would be raised into a certainty if we could demonstrate the phyletic development of the maggot-formed out of the caterpillar-formed Hymenopterous larvæ by means of the ontogeny of the former. From the beautiful investigations of Bütschli on the embryonic development of bees[27] we know that the embryo of the

[27] Zeitschrift für wissenschaftl. Zoologie, vol. xx. p. 519.

grub possesses a complete head, consisting of four segments and provided with the three typical pairs of jaws. These head segments do not subsequently become formed into a true horny head, but shrivel up; whilst the jaws disappear with the exception of the first pair, which are retained in the form of soft processes with small horny points. We know also that from the three foremost segments of the embryo the three typical pairs of legs are developed in the form of round buds, just as they first appear in all insects.[28] These rudimentary limbs undergo complete degeneration before the birth of the larva, as also do those of the whole[29] of the remaining segments, which, even in this primitive condition, show a small difference to the three foremost rudimentary legs.

The grub-like larvæ of the Hymenoptera have therefore descended from forms which possessed a horny head with antennæ and three pairs of gnathites and a 13-segmented body, of which the three foremost segments were provided with legs differing somewhat from those of the other segments; that is to say, they have descended from larvæ which possessed a structure generally similar to that of the existing saw-fly larvæ. The common derivation of all the Hymenoptera from one source is thus established with certainty.[30]

But upon what does this great inequality in the form-relationship of the larvæ and imagines depend? The existing maggot-like grubs are without doubt much further removed from the active caterpillar-like larvæ than are the saw-flies from the Aculeate Hymenoptera. Whilst these two groups differ only through various modifications of the typical parts (limbs, &c.), their larvæ are separable by much deeper-seated distinctions; limbs of typical importance entirely vanish in the one group, but in the other attain to complete development.

In the Hymenoptera there exists therefore a very considerable incongruence in the systems based morphologically, *i. e.* on the pure form-relationships of the larvæ and of the imagines. The reason of this is not difficult to find: *the conditions of life differ much less in the case of the imagines than in that of the larvæ*. In the former the conditions of life are similar in their broad features. Hymenoptera live chiefly in the air and fly by day, and in their mode of obtaining food do not present any considerable differences. Their larvæ, on the other hand, live under almost diametrically opposite conditions. Those of the saw-flies live after the manner of caterpillars upon or in plants, in both cases their peculiar locomotion being adapted for the acquisition and their masticatory organs for the reduction of food. The larvæ of the other Hymenoptera, however, do not as a rule require any means of locomotion for reaching nor any organs of mastication for swallowing their food, since they are fed in cells, like the bees and wasps, or grow up in plant galls of which they suck the juice, or are parasitic on other insects by whose blood they are nourished. We can readily comprehend that in the whole of this last group the legs should disappear, that the jaws should likewise vanish or should become diminished to one pair retained in a much reduced condition, that the horny casing of the head, the surface of attachment of the muscles of the jaws, should consequently be lost, and that even the segments of the head itself should become more or less shrivelled up as the organs of sense therein located became suppressed.

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[28] [See for instance Lubbock's "Origin and Metamorphoses of Insects," chap. iii.; and F. M. Balfour's "Comparative Embryology," vol. i., 1880, pp. 327 – 356. This last work contains an admirable *résumé* of our knowledge of the embryonic development of insects up to the date of publication. R.M.]

[29] Are not the 4th, 11th, and 12th segments destitute of the rudiments of legs as in the larvæ of all existing saw-flies? I might almost infer this from Bütschli's figures (see for instance Pl. XXV., Fig. 17A).

[30] [The grub-formed Hymenopterous larvæ, like the larvæ of all other holometabolous insects, thus represent an acquired degenerative stage in the development, *i. e.* an adaptation to the conditions of life at that stage. Bearing in mind the above-quoted observations of Bütschli and the caterpillar-like form of the Terebrantiate group of Hymenopterous larvæ, the following remarks of Balfour's (*loc. cit.* p. 353), appear highly suggestive: – "While in a general way it is clear that the larval forms of insects cannot be expected to throw much light on the nature of insect ancestors, it does nevertheless appear to me probable that such forms as the caterpillars of the Lepidoptera are not without a meaning in this respect. It is easy to conceive that even a secondary larval form may have been produced by the prolongation of one of the embryonic stages; and the general similarity of a caterpillar to *Peripatus*, and the retention by it of post-thoracic appendages, are facts which appear to favour this view of the origin of the caterpillar form." See also Sir John Lubbock, *loc. cit.*, pp. 93 and 95. R.M.]

Конец ознакомительного фрагмента.