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STUDIES IN THE THEORY OF DESCENT, VOLUME I

August Weismann

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Содержание

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PREFATORY NOTICE

The present work by Professor Weismann, well known for his profound embryological investigations on the Diptera, will appear, I believe, to every naturalist extremely interesting and well deserving of careful study. Any one looking at the longitudinal and oblique stripes, often of various and bright colours, on the caterpillars of Sphinx-moths, would naturally be inclined to doubt whether these could be of the least use to the insect; in the olden time they would have been called freaks of Nature. But the present book shows that in most cases the colouring can hardly fail to be of high importance as a protection. This indeed was proved experimentally in one of the most curious instances described, in which the thickened anterior end of the caterpillar bears two large ocelli or eye-like spots, which give to the creature so formidable an appearance that birds were frightened away. But the mere explanation of the colouring of these caterpillars is but a very small part of the merit of the work. This mainly consists in the light thrown on the laws of variation and of inheritance by the facts given and discussed. There is also a valuable discussion on classification, as founded on characters displayed at different ages by animals belonging to the same group. Several distinguished naturalists maintain with much confidence that organic beings tend to vary and to rise in the scale, independently of the conditions to which they and their progenitors have been exposed; whilst others maintain that all variation is due to such exposure, though the manner in which the environment acts is as yet quite unknown. At the present time there is hardly any question in biology of more importance than this of the nature and causes of variability, and the reader will find in the present work an able discussion on the whole subject, which will probably lead him to pause before he admits the existence of an innate tendency to perfectibility. Finally, whoever compares the discussions in this volume with those published twenty years ago on any branch of Natural History, will see how wide and rich a field for study has been opened up through the principle of Evolution; and such fields, without the light shed on them by this principle, would for long or for ever have remained barren.

Charles Darwin.

TRANSLATOR'S PREFACE

In offering to English readers this translation of Professor Weismann's well-known "Studies in the Theory of Descent," the main part of which is devoted to entomological subjects, I have been actuated by the desire of placing in the hands of English naturalists one of the most complete of recent contributions to the theory of Evolution as applied to the elucidation of certain interesting groups of facts offered by the insect world. Although many, if not most, working naturalists are already familiar with the results of Dr. Weismann's researches, of which abstracts have from time to time appeared in English and American scientific journals, I nevertheless believe that a study of the complete work, by enabling the reader to follow closely the detailed lines of reasoning and methods of experiment employed by the author, will be found to be of considerable value to those biologists who have not been able to follow the somewhat difficult phraseology of the original. It is not my intention, nor would it be becoming in me to discuss here the merits of the results arrived at by the minute and laborious investigations with which Dr. Weismann has for many years occupied himself. I may however point out that before the appearance of the present work the author, in addition to his well-known papers on the embryology and development of insects, had published two valuable contributions to the theory of descent, viz. one entitled "Über die Berechtigung der Darwin'schen Theorie" (1868), and another "Über den Einfluss der Isolirung auf die Artbildung" (1872). These works, which are perhaps not so well known in this country as could be desired, might be advantageously studied in connection with the present volume wherein they are frequently referred to.

Since every new contribution to science is a fresh starting-point for future work, I may venture without any great breach of propriety to dwell briefly upon one or two of the main points which appear to me to be suggested by Prof. Weismann's investigations.

Although the causes of Glacial Epochs is a subject which has much occupied the attention of geologists and physiographers, the question is one of such great complexity that it cannot yet be regarded as finally settled. But apart from the question of causes – a most able discussion of which is given by the author of "Island Life" – there is not the least doubt that at no very distant geological period there occurred such an epoch, which, although intermittent, was of considerable duration. The last great geological event which our globe experienced was in fact this Ice Age, and the pure naturalist has not hitherto attributed in my opinion sufficient importance to the *direct* modifying effects of this prolonged period of cold. It is scarcely possible that such a vast climatic change as that which came on at the close of the Pliocene Period should have left no permanent effect upon our present fauna and flora, all the species of which have survived from the glacial age. The great principle of Natural Selection leads us to see how pre-glacial forms may have become adapted to the new climatic conditions (which came on gradually) by the "survival of the fittest" or "indirect equilibration." The influence of the last Glacial Epoch as a factor in determining the present geographical distribution of animals and plants has already been amply treated of by many writers since the broad paths were traced out by Darwin, Lyell, and Wallace. The last-named author has indeed quite recently discussed this branch of the subject most exhaustively in his work on "Island Life" above mentioned. The reference of a particular group of phenomena – the seasonal dimorphism of butterflies – to the direct action of the Glacial Period and the subsequent influence of the ameliorating climate, was however the first step taken in this neglected field by the author of the present work in 1875. It is possible, and indeed probable, that future researches will show that other characters among existing species can be traced to the same causes.

The great generalizations of embryology, which science owes so largely to the researches of Karl Ernst von Baer, bear to the theory of descent the same relations that Kepler's laws bear to the theory of gravitation. These last-named laws are nothing more than generalized statements of the motions of the planets, which were devoid of meaning till the enunciation of the theory of gravitation. Similarly the generalized facts of embryology are meaningless except in the light of the theory of descent. It has now become a recognized principle in biology that animals in the course of their development from the ovum recapitulate more or less completely the phases through which their ancestors have passed. The practical application of this principle to the determination of the line of descent of any species or group of species is surrounded by difficulties, but attempts have been made of late years – as by Haeckel in his *Gastrula* theory – to push the law to its legitimate consequences. In this country Sir John Lubbock, in 1874, appealed to the embryonic characters of larvæ in support of his views on the origin of insects. To the author of this work (1876) is due the first application of the principle of Ontogeny as revealing the origin of the markings of caterpillars. A most valuable method of research is thus opened up, and entomologists should not be long in availing themselves of it. Our knowledge of the subject of larval development in Lepidoptera is still most imperfect, and it cannot as yet be foreseen to what extent the existing notions of classification in this much-studied order may have to be modified when a minute study of the Comparative Ontogeny of larval characters, worked out as completely as possible for each family, has enabled a true genealogical system to be drawn up. The extent to which such a larval genealogy would coincide with our present classification cannot now be decided, but he who approaches this fruitful line of inquiry in the true spirit of an investigator, will derive much instruction from Prof. Weismann's remarks on "Phyletic Parallelism in Metamorphic Species." The affinities of the larger groups among Lepidoptera would most probably be made out once and for ever if systematists would devote more time to observation in this field, and to the co-ordination and working up of the numerous data scattered throughout the vast number of entomological publications.

The doctrine of development by no means implies, as has sometimes been maintained, a continuous *advancement* in organization. Although the scale of organic nature has continued to rise as a whole, cases may occasionally occur where a *lower grade* of organization is better adapted to certain conditions of life. This principle of "degeneration" was recognized by Darwin as early as in the first edition of the "Origin of Species;" it was soon perceived to be applicable to the phenomenon of parasitism, and was first definitely formulated by Dr. Anton Dohrn in 1875. In a lecture delivered before the British Association at Sheffield in 1879, Prof. E. Ray Lankester ascribed to "degeneration" a distinct and well-defined function in the theory of descent. Dr. Weismann's explanation of the transformation of Axolotl given in the fourth essay of this work, may be regarded as a special contribution to this phase of Darwinism. Whilst refuting the idea held by certain naturalists, that such cases are arguments against the origin of species by the accumulation of minute variations, and prove the possibility of development *per saltum*, the theory here advanced (that *Siredon* at a former period existed at a higher stage of development as *Amblystoma*, and that the observed cases of metamorphosis are but reversions to this lost higher stage) suggests the question whether there may not still be in existence many other degenerated forms quite unsuspected by naturalists.

Many of the opponents of Evolution have from time to time denounced this doctrine as leading to "pure materialism," a denunciation which may appear somewhat alarming to the uninitiated, but which may not seem fraught with any serious consequences to those who have followed the course of philosophical speculation during the last few years. Those who attack the doctrine on this ground will however do well to consider Prof. Weismann's views set forth in the last essay in this volume, before hastily assuming that the much dreaded "materialism" is incompatible with any other conception of Nature.

The small amount of leisure time which I have been able to devote to the translation of this volume has delayed its completion considerably beyond the anticipated time, and it was with a view to meeting this difficulty that I departed from the original form of the German edition and issued it in parts. Owing to the extremely idiomatic character of the German text, I have throughout endeavoured to preserve only the author's meaning, regardless of literal translation or of the construction of the original. In some few cases, however, I have intentionally adopted literal translations of certain technical expressions which might, I think, be advantageously introduced into our biological vocabularies. Some alterations have been made in the original text by the author for the present edition, and many new notes have been added. For those bearing my initials I am alone responsible.

It gives me much pleasure in conclusion to express my thanks to Dr. Weismann, not only for the readily given permission to publish an English translation of his work, but also for much valuable assistance during the execution of the task. The author has been good enough to superintend the drawing of the plates for this edition, and he has also read through the greater part of the manuscript. From Mr. Darwin also I have received much kindly encouragement, and among entomologists I am especially indebted to Mr. W. H. Edwards of West Virginia, for his valuable additions to the first part. To my friends Mr. A. G. Butler, Mr. Roland Trimen, and Mr. F. Moore, I owe acknowledgments for much useful information concerning the caterpillars of exotic *Sphingidæ*, which I have incorporated in the notes and appendices, and Mr. W. S. Simpson has given me occasional advice in the translation of some of the more difficult passages.

R. M.

London, November, 1881.

PREFACE TO THE ENGLISH EDITION

With the appearance of Charles Darwin's work "On the Origin of Species," in the year 1858, there commenced a new era in biology. Weary of the philosophical speculations which, at the beginning of this century, had at first been started with moderation but had afterwards been pushed to excess, biologists had entirely let drop all general questions and confined themselves to special investigations. The consideration even of general questions had quite fallen into disuse, and the investigation of mere details had led to a state of intellectual shortsightedness, interest being shown only for that which was immediately in view. Immense numbers of detailed facts were thus accumulated, but they could not possibly be mastered; the intellectual bond which should have bound them together was wanting.

But all this was changed in a short time. At first only single and mostly the younger naturalists fell in with the new theory of development proclaimed by Darwin, but the conviction soon became general that this was the only scientifically justifiable hypothesis of the origin of the organic world.

The materials accumulated in all the provinces of biology now for the first time acquired a deeper meaning and significance; unexpected inter-relations revealed themselves as though spontaneously, and what formerly appeared as unanswerable enigmas now became clear and comprehensible. Since that time what a vast modification has the subject of animal embryology undergone; how full of meaning appear the youngest developmental stages, how important the larvæ; how significant are rudimentary organs; what department of biology has not in some measure become affected by the modifying influence of the new ideas!

But the doctrine of development not only enabled us to understand the facts already existing; it gave at the same time an impetus to the acquisition of unforeseen new ones. If at the present day we glance back at the development of the biological sciences within the last twenty years, we must be astonished both at the enormous array of new facts which have been evoked by the theory of development, and by the immense series of special investigations which have been called forth by this doctrine.

But while the development theory for by far the greater majority of these investigations served as a light which more and more illuminated the darkness of ignorance, there appeared at the same time some other researches in which this doctrine itself became the object of investigation, and which were undertaken with a view to establish it more securely.

To this latter class of work belong the "Studies" in the present volume.

It will perhaps be objected that the theory of descent has already been sufficiently established by Darwin and Wallace. It is true that their newly-discovered principle of selection is of the very greatest importance, since it solves the riddle as to how that which is useful can arise in a purely mechanical way. Nor can the transforming influence of direct action, as upheld by Lamarck, be called in question, although its extent cannot as yet be estimated with any certainty. The *secondary* modifications which Darwin regards as the consequence of a change in some other organ must also be conceded. But are these three factors actually competent to explain the complete transformation of one species into another? Can they transform more than mere single characters or groups of characters? Can we consider them as the sole causes of the regular phenomena of the development of the races of animals and plants? Is there not perhaps an unknown force underlying these numberless developmental series as the true motor power – a “developmental force” urging species to vary in certain directions and thus calling into existence the chief types and sub-types of the animal and vegetable kingdoms?

At the time these “Studies” first appeared (1875) they had been preceded by a whole series of attempts to introduce into science such an unknown power. The botanists, Nägeli and Askenasy, had designated it the “perfecting principle” or the “fixed direction of variation;” Kolliker as the “law of creation;” the philosophers, Von Hartmann and Huber, as the “law of organic development,” and also “the universal principle of organic nature.”

It was thus not entirely superfluous to test the capabilities of the known factors of transformation. We had here before us a question of the highest importance – a question which entered deeply into all our general notions, not only of the organic world, but of the universe as a whole.

This question – does there exist a special "developmental force"? – obviously cannot be decided by mere speculation; it must also be attempted to approach it by the inductive method.

The five essays in this volume are attempts to arrive, from various sides, somewhat nearer at a solution of the problem indicated.

The first essay on the "Seasonal Dimorphism of Butterflies" is certainly but indirectly connected with the question; it is therein attempted to discover the causes of this remarkable dimorphism, and by this means to indicate at the same time the extent of one of the transforming factors with reference to a definite case. The experiments upon which I base my views are not as numerous as I could desire, and if I were now able to repeat them they would be carried out more exactly than was possible at that time, when an experimental basis had first to be established. In spite of this, the conclusions to which I was led appear to be on the whole correct. That admirable and most conscientious observer of the North American butterflies, Mr. W. H. Edwards, has for many years experimented with American species in a manner similar to that which I employed for European species, and his results, which are published here in Appendix II. to the first essay, contain nothing as far as I can see which is not in harmony with my views. Many new questions suggest themselves, however, and it would be a grateful task if some entomologist would go further into these investigations.

The second essay directly attacks the main problem above indicated. It treats of the "Origin of the Markings of Caterpillars," and is to some extent a test of the correctness and capabilities of the Darwinian principles; it attempts to trace the differences in form in a definite although small group entirely to known factors.

Why the markings of caterpillars have particularly been chosen for this purpose will appear for two reasons.

The action of Natural Selection, on account of the nature of this agency, can only be exerted on those characters which are of biological importance. As it was to be tested whether, besides Natural Selection and the direct action of external conditions, together with the correlative results of these two factors, there might not lie concealed in the organism some other unknown transforming power, it was desirable to select for the investigation a group of forms which, if not absolutely excluding, nevertheless appeared possibly to restrict, the action of one of the two known factors of transformation, that of Natural Selection; a group of forms consisting essentially of so-called "purely morphological" characters, and not of those the utility of which was obvious, and of which the origin by means of Natural Selection was both possible and probable *ab initio*. Now, although the *colouring* can readily be seen to be of value to the life of its possessors, this is not the case with the quite independent *markings* of caterpillars; excepting perhaps those occasional forms of marking which have been regarded as special cases of protective resemblance. The markings of caterpillars must in general be considered as "purely morphological" characters, *i. e.* as characters which we do not know to be of any importance to the life of the species, and which cannot therefore be referred to Natural Selection. The most plausible explanation of these markings might have been that they were to be regarded as ornaments, but this view precludes the possibility of referring them either to Natural Selection or to the influence of direct changes in the environment.

The markings of caterpillars offered also another advantage which cannot be lightly estimated; they precluded from the first any attempt at an explanation by means of Sexual Selection. Although I am strongly convinced of the activity and great importance of this last process of selection, its effects cannot be estimated in any particular case, and the origin of a cycle of forms could never be clearly traced to its various factors, if Sexual Selection had also to be taken into consideration. Thus, we may fairly suppose that many features in the markings of butterflies owe their origin to Sexual Selection, but we are, at least at present, quite in the dark as to how many and which of these characters can be traced to this factor.

An investigation such as that which has been kept in view in this second essay would have been impracticable in the case of butterflies, as well as in the analogous case of the colouring and marking of birds, because it would have always been doubtful whether a character which did not appear to be attributable to any of the other transforming factors, should not be referred to Sexual Selection. It would have been impossible either to exclude or to infer an unknown developmental force, since we should have had to deal with two unknowns which could in no way be kept separate.

We escape this dilemma in the markings of caterpillars, because the latter do not propagate in this state. If the phenomena are not here entirely referable to Natural Selection and the direct action of the environment – if there remains an inexplicable residue, this cannot be referred to Sexual Selection, but to some as yet unknown power.

But it is not only in this respect that caterpillars offer especial advantages. If it is to be attempted to trace transformations in form to the action of the environment, an exact knowledge of this environment is in the first place necessary, *i. e.* a precise acquaintance with the conditions of life under the influence of which the species concerned exist. With respect to caterpillars, our knowledge of the life conditions is certainly by no means as complete as might be supposed, when we consider that hundreds of Lepidopterists have constantly bred and observed them during a most extended period. Much may have been observed, but it has not been thought worthy of publication; much has also been published, but so scattered and disconnected and at the same time of such unequal credibility, that a lifetime would be required to sift and collect it. A comprehensive biology of caterpillars, based on a broad ground, is as yet wanting, although such a labour would be both most interesting and valuable. Nevertheless, we know considerably more of the life of caterpillars than of any other larvæ, and as we are also acquainted with an immense number of species and are able to compare their life and the phenomena of their development, the subject of the markings of caterpillars must from this side also appear as the most favourable for the problem set before us.

To this must be added as a last, though not as the least, valuable circumstance, that we have here preserved to us in the development of the individual a fragment of the history of the species, so that we thus have at hand a means of following the course which the characters to be traced to their causes – the forms of marking – have taken during the lapse of thousands of years.

If with reference to the question as to the precise conditions of life in caterpillars I was frequently driven to my own observations, it was because I found as good as no previous work bearing upon this subject. It was well known generally that many caterpillars were differently marked and coloured when young to what they were when old; in some very striking cases brief notices of this fact are to be found in the works,[1]

[1] A most minute and exact description of the newly hatched larva of *Chionobas Aëllo* is given by the American entomologist, Samuel H. Scudder. Ann. Soc. Ent. de

more especially, of the older writers, and principally in that of the excellent observer Rösel von Rosenhof, the Nuremberg naturalist and miniature painter. In no single case, however, do the available materials suffice when we have to draw conclusions respecting the phyletic development. We distinctly see here how doubtful is the value of those observations which are made, so to speak, at random, *i. e.* without some definite object in view. Many of these observations may be both good and correct, but they are frequently wanting precisely in that which would make them available for scientific purposes. Thus everything had to be established *de novo*, and for this reason the investigations were extended over a considerable number of years, and had to be restricted to a small and as sharply defined a group as possible – a group which was easily surveyed, viz. that of the Hawk-moths or Sphinges.

Since the appearance of the German edition of this work many new observations respecting the markings of caterpillars have been published, such, for example, as those of W. H. Edwards and Fritz Müller. I have, however, made but little use of them here, as I had no intention of giving anything like a *complete* ontogeny of the markings in all caterpillars: larval markings were with me but means to an end, and I wished only to bring together such a number of facts as were necessary for drawing certain general conclusions. It would indeed be most interesting to extend such observations to other groups of Lepidoptera.

Belgique, xvi., 1873.

The third essay also, for similar reasons, is based essentially upon the same materials, viz. the Lepidoptera. It is therein attempted to approach the general problem – does there or does there not exist an internal transforming force? – from a quite different and, I may say, opposite point of view. The form-relationships of Lepidoptera in their two chief stages of development, imago and larva, are therein analysed, and by an examination of the respective forms it has been attempted to discover the nature of the causes which have led thereto.

I may be permitted to say that the fact here disclosed of a *different morphological*, with the *same genealogical* relationship, appears to me to be of decided importance. The agreement of the conclusions following therefrom with the results of the former investigation has, at least in my own mind, removed the last doubts as to the correctness of the latter.

The fourth and shortest essay on the "Transformation of the Axolotl into Amblystoma," starts primarily with the intention of showing that cases of sudden transformation are no proof of *per saltum* development. When this essay first appeared the view was still widely entertained that we had here a case proving *per saltum* development. That this explanation was erroneous is now generally admitted, but I believe that those who suppose that we have here to deal with some quite ordinary phenomenon which requires no explanation, now go too far towards the other extreme. The term "larval reproduction" is an *expression*, but no *explanation*; we have therefore to attempt to find out the true interpretation, but whether the one which I have given is correct must be judged of by others.

These four essays lead up to a fifth and concluding one "On the Mechanical Conception of Nature." Whilst the results obtained are here summed up, it is attempted to form them into a philosophical conception of Nature and of the Universe. It will be thought by many that this should have been left to professed philosophers, and I readily admit that I made this attempt with some misgiving. Two considerations, however, induced me to express here my own views. The first was that the facts of science are frequently misunderstood, or at any rate not estimated at their true value, by philosophers;[2] the second consideration was, that even certain naturalists and certainly very many non-naturalists, turn distrustfully from the results of science, because they fear that these would infallibly lead to a view of the Universe which is to them unacceptable, viz. the materialistic view. With regard to the former I wished to show that the views of the development of organic Nature inaugurated by Darwin and defended in this work are certainly correctly designated *mechanical*; with reference to the latter I wished to prove that such a mechanical conception of the organic world and of Nature in general, by no means leads merely to one single philosophical conception of Nature, viz. to Materialism, but that on the contrary it rather admits of legitimate development in a quite different manner.

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[2] I am aware that this certainly cannot be said of philosophers like Lotze or Herbert Spencer; but these are at the same time both naturalists and philosophers.

Thus in these last four essays much that appears heterogeneous will be found in close association, viz. scientific details and general philosophical ideas. In truth, however, these are most intimately connected, and the one cannot dispense with the other. As the detailed investigations of the three essays find their highest value in the general considerations of the fourth, and were indeed only possible by constantly keeping this end in view, so the general conclusions could only grow out of the results of the special investigations as out of a solid foundation. Had the new materials here brought together been already known, the reader would certainly have been spared the trouble of going into the details of special scientific research. But as matters stood it was indispensable that the facts should be examined into and established even down to the most trifling details. The essay "On the Origin of the Markings of Caterpillars" especially, had obviously to commence with the sifting and compilation of extensive morphological materials.

August Weismann.

Freiburg in Baden,
November, 1881.

Part I. ON THE SEASONAL DIMORPHISM OF BUTTERFLIES

I. The Origin and Significance of Seasonal Dimorphism

The phenomena here about to be subjected to a closer investigation have been known for a long period of time. About the year 1830 it was shown that the two forms of a butterfly (*Araschnia*) which had till that time been regarded as distinct, in spite of their different colouring and marking really belonged to the same species, the two forms of this dimorphic species not appearing simultaneously but at different seasons of the year, the one in early spring, the other in summer. To this phenomenon the term "seasonal dimorphism" was subsequently applied by Mr. A. R. Wallace, an expression of which the heterogeneous composition may arouse the horror of the philologist, but, as it is as concise and intelligible as possible, I propose to retain it in the present work.

The species of *Araschnia* through which the discovery of seasonal dimorphism was made, formerly bore the two specific names *A. Levana* and *A. Prorsa*. The latter is the summer and the former the winter form, the difference between the two being, to the uninitiated, so great that it is difficult to believe in their relationship. *A. Levana* (Figs. 1 and 2, Plate I.) is of a golden brown colour with black spots and dashes, while *A. Prorsa* (Figs. 5 and 6, Plate I.) is deep black with a broad white interrupted band across both wings. Notwithstanding this difference, it is an undoubted fact that both forms are merely the winter and summer generations of the same species. I have myself frequently bred the variety *Prorsa* from the eggs of *Levana*, and *vice versâ*.

Since the discovery of this last fact a considerable number of similar cases have been established. Thus P. C. Zeller[3] showed, by experiments made under confinement, that two butterflies belonging to the family of the 'Blues,' differing greatly in colour and marking, and especially in size, which had formerly been distinguished as *Plebeius* (*Lycæna*) *Polysperchon* and *P. Amyntas*, were merely winter and summer generations of the same species; and that excellent Lepidopterist, Dr. Staudinger, proved the same[4] with species belonging to the family of the 'Whites,' *Euchloe Belia* Esp. and *E. Ausonia* Hüb., which are found in the Mediterranean countries.

The instances are not numerous, however, in which the

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[3] "Über die Artrechte des *Polyommatus Amyntas* und *Polysperchon*." Stett. ent. Zeit. 1849. Vol. x. p. 177–182. [In Kirby's "Synonymic Catalogue of Diurnal Lepidoptera" *Plebeius Amyntas* is given as a synonym and *P. Polysperchon* as a var. of *P. Argiades* Pall. R.M.]

[4] "Die Arten der Lepidopteren-Gattung *Ino* Leach, nebst einigen Vorbemerkungen über Localvarietäten." Stett. ent. Zeit. 1862. Vol. xxiii. p. 342.

difference between the winter and summer forms of a species is so great as to cause them to be treated of in systematic work as distinct species. I know of only five of these cases. Lesser differences, having the systematic value of varieties, occur much more frequently. Thus, for instance, seasonal dimorphism has been proved to exist among many of our commonest butterflies belonging to the family of the 'Whites,' but the difference in their colour and marking can only be detected after some attention; while with other species, as for instance with the commonest of our small 'Blues,' *Plebeius Alexis* (= *Icarus*, Rott.), the difference is so slight that even the initiated must examine closely in order to recognize it. Indeed whole series of species might easily be grouped so as to show the transition from complete similarity of both generations, through scarcely perceptible differences, to divergence to the extent of varieties, and finally to that of species.

Nor are the instances of lesser differences between the two generations very numerous. Among the European diurnal Lepidoptera I know of about twelve cases, although closer observation in this direction may possibly lead to further discoveries.[5] Seasonal dimorphism occurs also in moths, although I am not in a position to make a more precise statement on this subject,[6] as my own observations refer only to butterflies.

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[5] [Eng. ed. W. H. Edwards has since pointed out several beautiful cases of seasonal dimorphism in America. Thus *Plebeius Pseudargiolus* is the summer form of *P. Violacea*, and *Phyciodes Tharos* the summer form of *P. Marcia*. See Edwards' "Butterflies of North America," 1868–79.]

[6] [Eng. ed. I learn by a written communication from Dr. Speyer that two Geometræ,

That other orders of insects do not present the same phenomenon depends essentially upon the fact that most of them produce only one generation in the year; but amongst the remaining orders there occur indeed changes of form which, although not capable of being regarded as pure seasonal dimorphism, may well have been produced in part by the same causes, as the subsequent investigation on the relation of seasonal dimorphism to alternation of generation and heterogenesis will more fully prove.

Now what are these causes?

Some years ago, when I imparted to a lepidopterist my intention of investigating the origin of this enigmatical dimorphism, in the hope of profiting for my inquiry from his large experience, I received the half-provoking reply: "But there is nothing to investigate: it is simply the specific character of this insect to appear in two forms; these two forms alternate with each other in regular succession according to a fixed law of Nature, and with this we must be satisfied." From his point of view the position was right; according to the old doctrine of species no question ought to be asked as to the causes of such

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Selenia Tetralunaria and *S. Illunaria* Hüb., are seasonally dimorphic. In both species the winter form is much larger and darker.] [*Selenia Lunaria*, *S. Illustraria*, and some species of *Ephyra* (*E. Punctaria* and *E. Omicronaria*) are likewise seasonally dimorphic. For remarks on the case of *S. Illustraria* see Dr. Knaggs in Ent. Mo. Mag., vol. iii. p. 238, and p. 256. Some observations on *E. Punctaria* were communicated to the Entomological Society of London by Professor Westwood in 1877, on the authority of Mr. B. G. Cole. See Proc. Ent. Soc. 1877, pp. vi, vii. R.M.]

phenomena in particular. I would not, however, allow myself to be thus discouraged, but undertook a series of investigations, the results of which I here submit to the reader.

The first conjecture was, that the differences in the imago might perhaps be of a secondary nature, and have their origin in the differences of the caterpillar, especially with those species which grow up during the spring or autumn and feed on different plants, thus assimilating different chemical substances, which might induce different deposits of colour in the wings of the perfect insect. This latter hypothesis was readily confuted by the fact, that the most strongly marked of the dimorphic species, *A. Levana*, fed exclusively on *Urtica major*. The caterpillar of this species certainly exhibits a well-defined dimorphism, but it is not seasonal dimorphism: the two forms do not alternate with each other, but appear mixed in every brood.

I have repeatedly reared the rarer golden-brown variety of the caterpillar separately, but precisely the same forms of butterfly were developed as from black caterpillars bred at the same time under similar external conditions. The same experiment was performed, with a similar result, in the last century by Rösel, the celebrated miniature painter and observer of nature, and author of the well-known "Insect Diversions" – a work in use up to the present day.

The question next arises, as to whether the causes originating the phenomena are not the same as those to which we ascribe the change of winter and summer covering in so many mammalia and birds – whether the change of colour and marking does not depend, in this as in the other cases, upon the *indirect action* of external conditions of life, i.e., on adaptation through natural selection. We are certainly correct in ascribing white coloration to adaptation[7]– as with the ptarmigan, which is white in winter and of a grey-brown in summer, both colours of the species being evidently of important use.

It might be imagined that analogous phenomena occur in butterflies, with the difference that the change of colour, instead of taking place in the same brood, alternates in different broods.[8] The nature of the difference which occurs in seasonal dimorphism, however, decidedly excludes this view; and moreover, the environment of butterflies presents such similar features, whether they emerge in spring or in summer, that all notions that we may be dealing with adaptational colours must be entirely abandoned.

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[7] [In 1860 Andrew Murray directed attention to the disguising colours of species which, like the Alpine hare, stoat, and ptarmigan, undergo seasonal variation of colour. See a paper "On the Disguises of Nature, being an inquiry into the laws which regulate external form and colour in plants and animals." Edinb. New Phil. Journ., Jan. 1860. In 1873 I attempted to show that these and other cases of "variable protective colouring" could be fairly attributed to natural selection. See Proc. Zoo. Soc., Feb. 4th, 1873, pp. 153–162. R.M.]

[8] [A phenomenon somewhat analogous to seasonal change of protecting colour does occur in some Lepidoptera, only the change, instead of occurring in the same individual, is displayed by the successive individuals of the same brood. See Dr. Wallace on *Bombyx Cynthia*, Trans. Ent. Soc. Vol. v. p. 485. R.M.]

I have elsewhere[9] endeavoured to show that butterflies in general are not coloured protectively during flight, for the double reason that the colour of the background to which they are exposed continually changes, and because, even with the best adaptation to the background, the fluttering motion of the wings would betray them to the eyes of their enemies.[10] I attempted also to prove at the same time that the diurnal Lepidoptera of our temperate zone have few enemies which pursue them when on the wing, but that they are subject to many attacks during their period of repose.

In support of this last statement I may here adduce an instance. In the summer of 1869 I placed about seventy specimens of *Araschnia Prorsa* in a spacious case, plentifully supplied with flowers. Although the insects found themselves quite at home, and settled about the flowers in very fine weather (one pair copulated, and the female laid eggs), yet I found some dead and mangled every morning. This decimation continued –

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9 "Über den Einfluss der Isolirung auf die Artbildung." Leipzig, 1872, pp. 55–62.

10 [Mr. A. R. Wallace maintains that the obscurely coloured females of those butterflies which possess brightly coloured males have been rendered inconspicuous by natural selection, owing to the greater need of protection by the former sex. See "Contributions to the Theory of Natural Selection," London, 1870, pp. 112–114. It is now generally admitted that the underside of butterflies has undergone protectional adaptation; and many cases of local variation in the colour of the underside of the wings, in accordance with the nature of the soil, &c., are known. See, for instance, Mr. D. G. Rutherford on the colour-varieties of *Aterica Meleagris* (Proc. Ent. Soc. 1878, p. xlii.), and Mr. J. Jenner Weir on a similar phenomenon in *Hipparchia Semele* (*loc. cit.* p. xlix.) R.M.]

many disappearing entirely without my being able to find their remains – until after the ninth day, when they had all, with one exception, been slain by their nocturnal foes – probably spiders and *Opilionidæ*.

Diurnal Lepidoptera in a position of rest are especially exposed to hostile attacks. In this position, as is well known, their wings are closed upright, and it is evident that the adaptational colours on the under side are displayed, as is most clearly shown by many of our native species.[11]

Now, the differences in the most pronounced cases of seasonal dimorphism – for example, in *Araschnia Levana*– are much less manifest on the *under* than on the *upper* side of the wing. The explanation by adaptation is therefore untenable; but I will not here pause to confute this view more completely, as I believe I shall be able to show the true cause of the phenomenon.

If seasonal dimorphism does not arise from the *indirect* influence of varying seasons of the year, it may result from the *direct* influence of the varying external conditions of life, which are, without doubt, different in the winter from those of the summer brood.

There are two prominent factors from which such an influence may be expected – temperature and duration of development, i.e., duration of the chrysalis period. The duration of the larval period need not engage our attention, as it is only very little

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[11] [The fact that moths which, like the Geometræ, rest by day with the wings spread out, are protectively marked on the *upper* side, fully corroborates this statement. R.M.]

shorter in the winter brood – at least, it was so with the species employed in the experiments.

Starting from these two points of view, I carried on experiments for a number of years, in order to find out whether the dual form of the species in question could be traced back to the direct action of the influences mentioned.

The first experiments were made with *Araschnia Levana*. From the eggs of the winter generation, which had emerged as butterflies in April, I bred caterpillars, and immediately after pupation placed them in a refrigerator, the temperature of the air of which was 8°-10° R. It appeared, however, that the development could not thus be retarded to any desired period by such a small diminution of temperature, for, when the box was taken out of the refrigerator after thirty-four days, all the butterflies, about forty in number, had emerged, many being dead, and others still living. The experiment was so far successful that, instead of the *Prorsa* form which might have been expected under ordinary circumstances, most of the butterflies emerged as the so-called *Porima* (Figs. 3, 4, 7, 8, and 9, Plate I.); that is to say, in a form intermediate between *Prorsa* and *Levana* sometimes found in nature, and possessing more or less the marking of the former, but mixed with much of the yellow of *Levana*.

It should be here mentioned, that similar experiments were made in 1864 by George Dorfmeister, but unfortunately I did not get this information[12] until my own were nearly completed. In these well-conceived, but rather too complicated experiments, the author arrives at the conclusion "that temperature certainly affects the colouring, and through it the marking, of the future butterfly, and chiefly so during pupation." By lowering the temperature of the air during a portion of the pupal period, the author was enabled to produce single specimens of *Porima*, but most of the butterflies retained the *Prorsa* form. Dorfmeister employed a temperature a little higher than I did in my first experiments, viz. 10°-11° R., and did not leave the pupæ long exposed, but after 5½-8 days removed them to a higher temperature. It was therefore evident that he produced transition forms in a few instances only, and that he never succeeded in bringing about a complete transformation of the summer into the winter form.

In my subsequent experiments I always exposed the pupæ to a temperature of 0°-1° R.; they were placed directly in the refrigerator, and taken out at the end of four weeks. I started with the idea that it was perhaps not so much the reduced temperature as the retardation of development which led to the transformation. But the first experiment had shown that the butterflies emerged between 8° and 10° R., and consequently that the development could not be retarded at this temperature.

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[12] "Über die Einwirkung verschiedener, während der Entwicklungsperioden angewendeter Wärmegrade auf die Färbung und Zeichnung der Schmetterlinge." A communication to the Society of Natural Science of Steiermark, 1864.

A very different result was obtained from the experiment made at a lower temperature.[13] Of twenty butterflies, fifteen had become transformed into *Porima*, and of these three appeared very similar to the winter form (*Levana*), differing only in the absence of the narrow blue marginal line, which is seldom absent in the true *Levana*. Five butterflies were uninfluenced by the cold, and remained unchanged, emerging as the ordinary summer form (*Prorsa*). It thus appeared from this experiment, that a large proportion of the butterflies inclined to the *Levana* form by exposure to a temperature of 0°-1° R. for four weeks, while in a few specimens the transformation into this form was nearly perfect.

Should it not be possible to perfect the transformation, so that each individual should take the *Levana* form? If the assumption of the *Prorsa* or *Levana* form depends only on the direct influence of temperature, or on the duration of the period of development, it should be possible to compel the pupæ to take one or the other form at pleasure, by the application of the necessary external conditions. This has never been accomplished with *Araschnia Prorsa*. As in the experiment already described, and in all subsequent ones, single specimens appeared as the unchanged summer form, others showed an appearance of transition, and but very few had changed so completely as to be possibly taken for the pure *Levana*. In some species of the sub-family *Pierinæ*, however, at least in the case of the summer

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[13] See Exp. 9, Appendix I.

brood, there was, on the contrary, a complete transformation.

Most of the species of our 'Whites' (*Pierinæ*) exhibit the phenomenon of seasonal dimorphism, the winter and summer forms being remarkably distinct. In *Pieris Napi* (with which species I chiefly experimented) the winter form (Figs. 10 and 11, Plate I.) has a sprinkling of deep black scales at the base of the wings on the upper side, while the tips are more grey, and have in all cases much less black than in the summer form; on the underside the difference lies mainly in the frequent breadth, and dark greenish-black dusting, of the veins of the hind wings in the winter form, while in the summer form these greenish-black veins are but faintly present.

I placed numerous specimens of the summer brood, immediately after their transformation into chrysalides, in the refrigerator (0°-1° R.), where I left them for three months, transferring them to a hothouse on September 11th, and there (from September 26th to October 3rd) sixty butterflies emerged, the whole of which, without exception – and most of them in an unusually strong degree – bore the characters of the winter form. I, at least, have never observed in the natural state such a strong yellow on the underside of the hind wings, and such a deep blackish-green veining, as prevailed in these specimens (see, for instance, Figs. 10 and 11). The temperature of the hothouse (12°-24° R.) did not, however, cause the emergence of the whole of the pupæ; a portion hibernated, and produced in the following spring butterflies of the winter form only. I thus succeeded, with this species of *Pieris*, in completely changing every individual of the summer generation into the winter form.

It might be expected that the same result could be more readily obtained with *A. Levana*, and fresh experiments were undertaken, in order that the pupæ might remain in the refrigerator fully two months from the period of their transformation (9–10th July). But the result obtained was the same as before – fifty-seven butterflies emerged in the hothouse[14] from September 19th to October 4th, nearly all of these approaching very near to the winter form, without a single specimen presenting the appearance of a perfect *Levana*, while three were of the pure summer form (*Prorsa*).

Thus with *Levana* it was not possible, by refrigeration and retardation of development, to change the summer completely into the winter form in all specimens. It may, of course, be objected that the period of refrigeration had been too short, and that, instead of leaving the pupæ in the refrigerator for two months, they should have remained there six months, that is, about as long as the winter brood remains under natural conditions in the chrysalis state. The force of this last objection must be recognized, notwithstanding the improbability that the desired effect would be produced by a longer period of cold, since the doubling of this period from four to eight weeks did not produce[15] any decided increase in the strength of

[14] See Exp. 11, Appendix I.

[15] See Exps. 4, 9, and 11, Appendix I.

the transformation. I should not have omitted to repeat the experiment in this modified form, but unfortunately, in spite of all trouble, I was unable to collect during the summer of 1873 a sufficient number of caterpillars. But the omission thus caused is of quite minor importance from a theoretical point of view.

For let us assume that the omitted experiment had been performed – that pupæ of the summer brood were retarded in their development by cold until the following spring, and that every specimen then emerged in the perfect winter form, Levana. Such a result, taken in connexion with the corresponding experiment upon *Pieris Napi*, would warrant the conclusion that the direct action of a certain amount of cold (or of retardation of development) is able to compel all pupæ, from whichever generation derived, to assume the winter form of the species. From this the converse would necessarily follow, viz. that a certain amount of warmth would lead to the production of the summer form, *Prorsa*, it being immaterial from which brood the pupæ thus exposed to warmth might be derived. But the latter conclusion was proved experimentally to be incorrect, and thus the former falls with it, whether the imagined experiment with *Prorsa* had succeeded or not.

I have repeatedly attempted by the application of warmth to change the winter into the summer form, but always with the same negative result. *It is not possible to compel the winter brood to assume the form of the summer generation.*

A. Levana may produce not only two but three broods in the year, and may, therefore, be said to be *polygoneutic*.[16] One winter brood alternates with two summer broods, the first of which appears in July, and the second in August. The latter furnishes a fourth generation of pupæ, which, after hibernation, emerge in April, as the first brood of butterflies in the form *Levana*.

I frequently placed pupæ of this fourth brood in the hothouse immediately after their transformation, and in some cases even during the caterpillar stage, the temperature never falling, even at night, below 12° R., and often rising during the day to 24° R. The result was always the same: all, or nearly all, the pupæ hibernated, and emerged the following year in the winter form as perfectly pure *Levana*, without any trace of transition to the *Prorsa* form. On one occasion only was there a *Porima* among them, a case for which an explanation will, I believe, be found later on. It often happened, on the other hand, that some few of the butterflies emerged in the autumn, about fourteen days after pupation; and these were always *Prorsa* (the summer form), excepting once a *Porima*.

From these experiments it appeared that similar causes (heat) affect different generations of *A. Levana* in different manners. With both summer broods a high temperature always caused the appearance of *Prorsa*, this form arising but seldom from the third brood (and then only in a few individuals), while the

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16 It seems to me very necessary to have a word expressing whether a species produces one, two, or more generations in the year, and I have therefore coined the expression *mono-*, *di-*, and *polygoneutic* from γονεύω, I produce.

greater number retained the *Levana* form unchanged. We may assign as the reason for this behaviour, that the third brood has no further tendency to be accelerated in its development by the action of heat, but that by a longer duration of the pupal stage the *Levana* form must result. On one occasion the chrysalis stage was considerably shortened in this brood by the continued action of a high temperature, many specimens thus having their period of development reduced from six to three months. The supposed explanation above given is, however, in reality no explanation at all, but simply a restatement of the facts. The question still remains, why the third brood in particular has no tendency to be accelerated in its development by the action of heat, as is the case with both the previous broods?

The first answer that can be given to this question is, that the cause of the different action produced by a similar agency can only lie in the *constitution*, i.e., in the *physical nature* of the broods in question, and not in the external influences by which they are acted upon. Now, what is the difference in the physical nature of these respective broods? It is quite evident, as shown by the experiments already described, that cold and warmth cannot be the *immediate* causes of a pupa emerging in the *Prorsa* or *Levana* form, since the last brood always gives rise to the *Levana* form, whether acted on by cold or warmth. The first and second broods only can be made to partly assume, more or less completely, the *Levana* form by the application of cold. In these broods then, a low temperature is the *mediate* cause of the transformation into the *Levana* form.

The following is my explanation of the facts. The form *Levana* is the original type of the species, and *Prorsa* the secondary form arising from the gradual operation of summer climate. When we are able to change many specimens of the summer brood into the winter form by means of cold, this can only depend upon reversion to the original, or ancestral, form, which reversion appears to be most readily produced by cold, that is, by the same external influences as those to which the original form was exposed during a long period of time, and the continuance of which has preserved, in the winter generations, the colour and marking of the original form down to the present time.

I consider the origination of the *Prorsa* from the *Levana* form to have been somewhat as follows: – It is certain that during the diluvial period in Europe there was a so-called 'glacial epoch,' which may have spread a truly polar climate over our temperate zone; or perhaps a lesser degree of cold may have prevailed with increased atmospheric precipitation. At all events, the summer was then short and comparatively cold, and the existing butterflies could have only produced one generation in the year; in other words, they were *monogoneutic*. At that time *A. Levana* existed only in the *Levana* form.[17] As the climate

[17] [Eng. ed. In the German edition, which appeared in 1874, I was not able to support this hypothesis by geographical data, and could then only ask the question "whether in the most northern portion of its area of distribution, appears in two or only in one generation?" This question is now answered by the Swedish Expedition to the Yenisei in 1876. Herr Philipp Trybom, one of the members of this expedition, observed

gradually became warmer, a period must have arrived when the summer lasted long enough for the interpolation of a second brood. The pupæ of *Levana*, which had hitherto hibernated through the long winter to appear as butterflies in the following

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A. Levana at the end of June and beginning of July, in the middle of Yenisei, in 60°-63° N. (Dagfjärilar från Yenisei in Översigt ap k. Vertensk. Akad. Förhandlingon, 1877, No. 6.) Trybom found *Levana* at Yenisk on June 23rd, at Worogova (61° 5´) on July 3rd, at Asinova (61° 25´) on July 4th, at Insarowa (62° 5´) on July 7th, and at Alinskaja (63° 25´) on July 9th. The butterflies were especially abundant at the beginning of June, and were all of the typical *Levana* form. Trybom expressly states, "we did not find a single specimen which differed perceptibly from Weismann's Figs. 1 and 2 ('Saison-Dimorphismus' Taf. I.)."The Swedish expedition soon left the Yenisei, and consequently was not able to decide by observations whether a second generation possessing the *Prorsa* form appeared later in the summer. Nevertheless, it may be stated with great probability that this is not the case. The districts in which *Levana* occurs on the Yenisei have about the same isotherm as Archangel or Haparanda, and therefore the same summer temperature. Dr. Staudinger, whose views I solicited, writes to me: – "In Finnmark (about 67° N.) I observed no species with two generations; even *Polyommatus Phlæas*, which occurs there, and which in Germany has always two, and in the south, perhaps, three generations, in Finnmark has only one generation. A second generation would be impossible, and this would also be the case with *Levana* in the middle of Yenisei. I certainly have *Levana* and *Prorsa* from the middle of Amur, but *Levana* flies there at the end of May, and the summers are very warm." The middle of Amur lies, moreover, in 50° N. lat., and therefore 10°-13° south of the districts of the Yenisei mentioned.It must thus be certainly admitted that on the Yenisei *A. Levana* occurs only in the *Levana* form, and that consequently this species is at the present time, in the northernmost portion of its area of distribution, in the same condition as that in which I conceive it to have been in mid Europe during the glacial period. It would be of the greatest interest to make experiments in breeding with this single-brooded *Levana* from the Yenisei, i.e., to attempt to change its offspring into the *Prorsa* form by the action of a high temperature. If this could not be accomplished it would furnish a confirmation of my hypothesis than which nothing more rigorous could be desired.]

summer, were now able to appear on the wing as butterflies during the same summer as that in which they left their eggs as larvæ, and eggs deposited by the last brood produced larvæ which fed up and hibernated as pupæ. A state of things was thus established in which the first brood was developed under very different climatic conditions from the second. So considerable a difference in colour and marking between the two forms as we now witness could not have arisen suddenly, but must have done so gradually. It is evident from the foregoing experiments that the *Prorsa* form did not originate suddenly. Had this been the case it would simply signify that every individual of this species possessed the faculty of assuming two different forms according as it was acted on by warmth or cold, just in the same manner as litmus-paper becomes red in acids and blue in alkalies. The experiments have shown, however, that this is not the case, but rather that the last generation bears an ineradicable tendency to take the *Levana* form, and is not susceptible to the influence of warmth, however long continued; while both summer generations, on the contrary, show a decided tendency to assume the *Prorsa* form, although they certainly can be made to assume the *Levana* form in different degrees by the prolonged action of cold.

The conclusion seems to me inevitable, that the origination of the *Prorsa* form was gradual – that those changes which originated in the chemistry of the pupal stage, and led finally to the *Prorsa* type, occurred very gradually, at first perhaps remaining completely latent throughout a series of generations, then very slight changes of marking appearing, and finally, after a long period of time, the complete *Prorsa* type was produced. It appears to me that the quoted results of the experiments are not only easily explained on the view of the *gradual* action of climate, but that this view is the only one admissible. The action of climate is best comparable with the so-called cumulative effect of certain drugs on the human body; the first small dose produces scarcely any perceptible change, but if often repeated the effect becomes cumulative, and poisoning occurs.

This view of the action of climate is not at all new, most zoologists having thus represented it; only the formal proof of this action is new, and the facts investigated appear to me of special importance as furnishing this proof. I shall again return to this view in considering climatic varieties, and it will then appear that also the nature of the transformation itself confirms the slow operation of climate.

During the transition from the glacial period to the present climate *A. Levana* thus gradually changed from a monogoneutic to a digoneutic species, and at the same time became gradually more distinctly dimorphic, this character originating only through the alteration of the summer brood, the primary colouring and marking of the species being retained unchanged by the winter brood. As the summer became longer a third generation could be interpolated – the species became polygoneutic; and in this manner two summer generations alternated with one winter generation.

We have now to inquire whether facts are in complete accordance with this theory – whether they are never at variance with it – and whether they can all be explained by it. I will at once state in anticipation, that this is the case to the fullest extent.

In the first place, the theory readily explains why the summer but not the winter generations are capable of being transformed; the latter cannot possibly revert to the *Prorsa* form, because this is much the younger. When, however, it happens that out of a hundred cases there occurs one in which a chrysalis of the winter generation, having been forced by warmth, undergoes transformation before the commencement of winter, and emerges in the summer form,[18] this is not in the least inexplicable. It cannot be atavism which determines the direction of the development; but we see from such a case that the changes in the first two generations have already produced a certain alteration in the third, which manifests itself in single cases under favourable conditions (the influence of warmth) by the assumption of the *Prorsa* form; or, as it might be otherwise expressed, the *alternating* heredity (of which we shall speak further), which implies the power of assuming the *Prorsa* form, remains latent as a rule in the winter generation, but becomes *continuous* in single individuals.

It is true that we have as yet no kind of insight into the nature of heredity, and this at once shows the defectiveness of

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[18] See Exp. 10, Appendix I.

the foregoing explanation; but we nevertheless know many of its external phenomena. We know for certain that one of these consists in the fact that peculiarities of the father do not appear in the son, but in the grandson, or still further on, and that they may be thus transmitted in a latent form. Let us imagine a character so transmitted that it appears in the first, third, and fifth generations, remaining latent in the intermediate ones; it would not be improbable, according to previous experiences, that the peculiarity should exceptionally, i.e., from a cause unknown to us, appear in single individuals of the second or fourth generation. But this completely agrees with those cases in which "exceptional" individuals of the winter brood took the *Prorsa* form, with the difference only that a cause (warmth) was here apparent which occasioned the development of the latent characters, although we are not in a position to say in what manner heat produces this action. These exceptions to the rule are therefore no objection to the theory. On the contrary, they give us a hint that after one *Prorsa* generation had been produced, the gradual interpolation of a second *Prorsa* generation may have been facilitated by the existence of the first. I do not doubt that even in the natural state single individuals of *Prorsa* sometimes emerge in September or October; and if our summer were lengthened by only one or two months this might give rise to a third summer brood (just as a second is now an accomplished fact), under which circumstances they would not only emerge, but would also have time for copulation and for depositing eggs, the larvæ from which would have time to grow up.

A sharp distinction must be made between the first establishment of a new climatic form and the transference of the latter to newly interpolated generations. The former always takes place very slowly; the latter may occur in a shorter time.

With regard to the duration of time which is necessary to produce a new form by the influence of climate, or to transmit to a succeeding generation a new form already established, great differences occur, according to the physical nature of the species and of the individual. The experiments with *Prorsa* already described show how diverse are individual proclivities in this respect. In Experiment No. 12 it was not possible out of seventy individuals to substitute *Prorsa* for the *Levana* form, even in one solitary case, or, in other words, to change alternating into continuous inheritance; whilst in the corresponding experiments of former years (Experiment 10, for example), out of an equal number of pupæ three emerged as *Prorsa*, and one as *Porima*. We might be inclined to seek for the cause of this different behaviour in external influences, but we should not thus arrive at an explanation of the facts. We might suppose, for instance, that a great deal depended upon the particular period of the pupal stage at which the action of the elevated temperature began – whether on the first, the thirtieth, or the hundredth day after pupation – and this conjecture is correct in so far that in the two last cases warmth can have no further influence than that of somewhat accelerating the emergence of the butterflies, but cannot change the *Levana* into the *Prorsa* form. I have repeatedly exposed a large number of *Levana* pupæ of the third generation to the temperature of an apartment, or even still higher (26° R.), during winter, but no *Prorsa* were obtained.[19]

But it would be erroneous to assume a difference in the action of heat according as it began on the first or third day after transformation; whether during or before pupation. This is best proved by Experiment No. 12, in which caterpillars of the fourth generation were placed in the hothouse several days before they underwent pupation; still, not a single butterfly assumed the *Prorsa* form. I have also frequently made the reverse experiment, and exposed caterpillars of the first summer brood to cold during the act of pupation. A regular consequence was the dying off of the caterpillars, which is little to be wondered at, as the sensitiveness of insects during ecdysis is well known, and transformation into the pupal state is attended by much deeper changes.

Dorfmeister thought that he might conclude from his experiments that temperature exerts the greatest influence in the first place during the act of pupation, and in the next place immediately after that period. His experiments were made, however, with such a small number of specimens that scarcely

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[19] When Dorfmeister remarks that hibernating pupæ which, at an early stage "were taken for development into a room, or not exposed to any cold, gave dwarfed, weakly and crippled," or otherwise damaged butterflies, this is entirely attributable to the fact that this able entomologist had neglected to supply the necessary moisture to the warm air. By keeping pupæ over water I have always obtained very fine butterflies.

any safe conclusion can be founded on them; still, this conclusion may be correct, in so far as everything depends on whether, from the beginning, the formative processes in the pupa tended to this or that direction, the final result of which is the *Prorsa* or *Levana* form. If once there is a tendency to one or the other direction, then temperature might exert an accelerating or a retarding influence, but the tendency cannot be further changed.

It is also possible – indeed, probable – that a period may be fixed in which warmth or cold might be able to divert the original direction of development most easily; and this is the next problem to be attacked, the answer to which, now that the main points have been determined, should not be very difficult. I have often contemplated taking the experiments in hand myself, but have abandoned them, because my materials did not appear to me sufficiently extensive, and in all such experiments nothing is to be more avoided than a frittering away of experimental materials by a too complicated form of problem.

There may indeed be a period most favourable for the action of temperature during the first days of the pupal stage; it appears from Experiment No. 12 that individuals tend in different degrees to respond to such influences, and that the disposition to abandon the ordinary course of development is different in different individuals. In no other way can it be explained that, in all the experiments made with the first and second generations of *Prorsa*, only *a portion* of the pupæ were compelled by cold to take the direction of development of *Levana*, and that even from the former only a few individuals completely reverted, the majority remaining intermediate.

If it be asked why in the corresponding experiments with *Pieris Napi* complete reversion always occurred without exception, it may be supposed that in this species the summer form has not been so long in existence, and that it would thus be more easily abandoned; or, that the difference between the two generations has not become so distinct, which further signifies that here again the summer form is of later origin. It might also be finally answered, that the tendency to reversion in different species may vary just as much as in different individuals of the same species. But, in any case, the fact is established that all individuals are impelled by cold to complete reversion, and that in these experiments it does not depend so particularly upon the moment of development when cold is applied, but that differences of individual constitution are much more the cause why cold brings some pupæ to complete, and others to partial, reversion, while yet others are quite uninfluenced. In reference to this, the American *Papilio Ajax* is particularly interesting.

This butterfly, which is somewhat similar to the European *P. Podalirius*, appears, wherever it occurs, in three varieties, designated as var. *Telamonides*, var. *Walshii*, and var. *Marcellus*. The distinguished American entomologist, W. H. Edwards, has proved by breeding experiments, that all three forms belong to the same cycle of development, and in such a manner that the first two appear only in spring, and always come only from hibernating pupæ, while the last form, var. *Marcellus*, appears only in summer, and then in three successive generations. A seasonal dimorphism thus appears which is combined with ordinary dimorphism, winter and summer forms alternating with each other; but the first appears itself in two forms or varieties, vars. *Telamonides* and *Walshii*. If for the present we disregard this complication, and consider these two winter forms as one, we should thus have four generations, of which the first possesses the winter form, and the three succeeding ones have, on the other hand, the summer form, var. *Marcellus*.

The peculiarity of this species consists in the fact that in all three summer generations only a portion of the pupæ emerge after a short period (fourteen days), whilst another and much smaller portion remains in the pupal state during the whole summer and succeeding winter, first emerging in the following spring, and then always in the winter form. Thus, Edwards states that out of fifty chrysalides of the second generation, which had pupated at the end of June, forty-five *Marcellus* butterflies appeared after fourteen days, whilst five pupæ emerged in April of the following year, and then as *Telamonides*.

The explanation of these facts is easily afforded by the foregoing theory. According to this, both the winter forms must be regarded as primary, and the *Marcellus* form as secondary. But this last is not yet so firmly established as *Prorsa*, in which reversion of the summer generations to the *Levana* form only occurs through special external influences; whilst in the case of

Ajax some individuals are to be found in every generation, the tendency of which to revert is still so strong that even the greatest summer heat is unable to cause them to diverge from their original inherited direction of development, or to accelerate their emergence and compel them to assume the *Marcellus* form. It is here beyond a doubt that it is not different external influences, but internal causes only, which maintain the old hereditary tendency, for all the larvæ and pupæ of many different broods were simultaneously exposed to the same external influences. But, at the same time, it is evident that these facts are not opposed to the present theory; on the contrary, they confirm it, inasmuch as they are readily explained on the basis of the theory, but can scarcely otherwise be understood.

If it be asked what significance attaches to the duplication of the winter form, it may be answered that the species was already dimorphic at the time when it appeared in only one annual generation. Still, this explanation may be objected to, since a dimorphism of this kind is not at present known, though indeed some species exhibit a sexual dimorphism,[20] in which one sex (as, for instance, the case of the female *Papilio Turnus*) appears in two forms of colouring, but not a dimorphism, as is here the

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[20] [For other remarkable cases of sexual dimorphism (not *antigeny* in the sense used by Mr. S. H. Scudder, Proc. Amer. Acad., vol. xii. 1877, pp. 150–158) see Wallace "On the Phenomena of Variation and Geographical Distribution, as illustrated by the Papilionidæ of the Malayan Region," Trans. Linn. Soc., vol. xxv. 1865, pp. 5–10. R.M.]

case, displayed by both sexes.[21] Another suggestion, therefore, may perhaps be offered.

In *A. Levana* we saw that reversion occurred in very different degrees with different individuals, seldom attaining to the true *Levana* form, and generally only reaching the intermediate form known as *Porima*. Now it would, at all events, be astonishing if with *P. Ajax* the reversion were always complete, as it is precisely in this case that the tendency to individual reversion is so variable. I might, for this reason, suppose that one of the two winter forms, viz. the var. *Walshii*, is nothing else than an incomplete reversion-form, corresponding to *Porima* in the case of *A. Levana*. Then *Telamonides* only would be the original form of the butterfly, and this would agree with the fact that this variety appears later in the spring than *Walshii*. Experiments ought to be able to decide this.[22] The pupæ of the first three generations placed upon

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[21] [Eng. ed. Dimorphism of this kind has since been made known: the North American *Limenitis Artemis* and *L. Proserpina* are not two species, as was formerly believed, but only one. Edwards bred both forms from eggs of *Proserpina*. Both are single-brooded, and both have males and females. The two forms fly together, but *L. Artemis* is much more widely distributed, and more abundant than *L. Proserpina*. See "Butterflies of North America," vol. ii.]

[22] [Eng. ed. Edwards has since proved experimentally that by the application of ice a large proportion of the pupæ do indeed give rise to the var. *Telamonides*. He bred from eggs of *Telamonides* 122 pupæ, which, under natural conditions, would nearly all have given the var. *Marcellus*. After two months' exposure to the low temperature there emerged from August 24th to October 16th, fifty butterflies, viz. twenty-two *Telamonides*, one intermediate form between *Telamonides* and *Walshii*, eight intermediate forms between *Telamonides* and *Marcellus* more nearly related to the former, six intermediate forms between *Telamonides* and *Marcellus*, but more

ice should give, for the greater part, the form *Telamonides*, for the lesser portion *Walshii*, and for only a few, or perhaps no individuals, the form *Marcellus*. This prediction is based on the view that the tendency to revert is on the whole great; that even with the first summer generation, which was the longest exposed to the summer climate, a portion of the pupæ, without artificial means, always emerged as *Telamonides*, and another portion as *Marcellus*. The latter will perhaps now become *Walshii* by the application of cold.

One would expect that the second and third generations would revert more easily, and in a larger percentage, than the first, because this latter first acquired the new *Marcellus* form; but the present experiments furnish no safe conclusion on this point. Thus, of the first summer generation only seven out of sixty-seven pupæ hibernated, and these gave *Telamonides*; while of the second generation forty out of seventy-six, and of the third generation twenty-nine out of forty-two pupæ hibernated. But to establish safer conclusions, a still larger number of experiments is necessary. According to the experience thus far gained, one might perhaps still be inclined to imagine that, with seasonal dimorphism, external influences operating on the individual

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closely resembling the latter, and thirteen *Marcellus*. Through various mishaps the action of the ice was not complete and equal. See the "Canadian Entomologist," 1875, p. 228. In the newly discovered case of *Phyciodes Tharos* also, Edwards has succeeded in causing the brood from the winter form to revert, by the application of ice to this same form. See Appendix II. for a *résumé* of Edwards' experiments upon both *Papilio Ajax* and *Phyciodes Tharos*. R.M.]

might directly compel it to assume one or the other form. I long held this view myself, but it is, nevertheless, untenable. That cold does not produce the one kind of marking, and warmth the other, follows from the before-mentioned facts, viz. that in *Papilio Ajax* every generation produces both forms; and, further, in the case of *A. Levana* I have frequently reared the fourth (hibernating) generation entirely in a warm room, and yet I have always obtained the winter form. Still, one might be inclined not to make the temperature *directly* responsible, but rather the retardation or acceleration of development produced through the action of temperature. I confess that I for a long time believed that in this action I had found the true cause of seasonal dimorphism. Both with *A. Levana* and *P. Napi* the difference between the duration of the pupal period in the winter and summer forms is very great, lasting as a rule, in the summer generation of *A. Levana*, from seven to twelve days, and in the winter generation about two hundred days. In this last species the pupal state can certainly be shortened by keeping them at an elevated temperature; but I have, nevertheless, only in one case obtained two or three butterflies at the end of December from caterpillars that had pupated in September, these generally emerging in the course of February and March, and are to be seen on the wing in warm weather during the latter month. The greatest reduction of the pupal period still leaves for this stage more than 100 days.

From this last observation it follows that it is not the duration of development which, in individual cases, determines the form of the butterfly, and which consequently decides whether the winter or summer form shall emerge, but that, on the contrary, the duration of the pupal stage is dependent on the tendency which the forthcoming butterfly had taken in the chrysalis state. This can be well understood when we consider that the winter form must have had a long, and the summer form a short pupal period, during innumerable generations. In the former the habit of slow development must have been just as well established as that of rapid development in the latter; and we cannot be at all surprised if we do not see this habit abandoned by the winter form when the opportunity presents itself. But that it may be occasionally abandoned the more proves that the duration of the pupal development less determines the butterfly form than does the temperature directly, in individual cases.

Thus, for instance, Edwards explicitly states that, whereas the two winter forms of *P. Ajax*, viz. the vars. *Walshii* and *Telamonides*, generally appear only after a pupal period of 150 to 270 days, yet individual cases occur in which the pupal stage is no longer than in the summer form, viz. fourteen days.[23] A similar thing occurs with *A. Levana*, for, as already explained, not only may the development of the winter form be forced to a certain degree by artificial warmth, but the summer generation frequently produces reversion-forms without

[23] Thus from eggs of *Walshii*, laid on April 10th, Edwards obtained, after a pupal period of fourteen days, from the 1st to the 6th of June, fifty-eight butterflies of the form *Marcellus*, one of *Walshii*, and one of *Telamonides*.

protraction of development. The intermediate reversion-form *Porima* was known long before it was thought possible that it could be produced artificially by the action of cold; it appears occasionally, although very rarely, at midsummer in the natural state.

If, then, my explanation of the phenomena is correct, the winter form is primary and the summer the secondary form, and those individuals which, naturally or artificially, assume the winter form must be considered as cases of atavism. The suggestion thus arises whether low temperature alone is competent to bring about this reversion, or whether other external influences are not also effective. Indeed, the latter appears to be the case. Besides purely internal causes, as previously pointed out in *P. Ajax*, warmth and mechanical motion appear to be able to bring about reversion.

That an unusually high temperature may cause reversion, I conclude from the following observation. In the summer of 1869 I bred the first summer brood of *A. Levana*; the caterpillars pupated during the second half of June, and from that time to their emergence, on 28th June–3rd July, great heat prevailed. Now, while the intermediate form *Porima* had hitherto been a great rarity, both in the free state and when bred, having never obtained it myself, for example, out of many hundreds of specimens, there were among the sixty or seventy butterflies that emerged from the above brood, some eight to ten examples of *Porima*. This is certainly not an exact experiment, but there seems to me a certain amount of probability that the high summer temperature in this case brought about reversion.

Neither for the second cause to which I have ascribed the power of producing reversion can I produce any absolute evidence, since the experimental solution of all these collateral questions would demand an endless amount of time. I am in possession of an observation, however, which makes it appear probable to me that continuous mechanical movement acts on the development of the pupæ in a similar manner to cold, that is, retarding them, and at the same time producing reversion. I had, in Freiburg, a large number of pupæ of the first summer brood of *Pieris Napi*, bred from eggs. I changed residence while many caterpillars were in course of transformation and travelled with the pupæ in this state seven hours by rail. Although this brood of *P. Napi*, under ordinary circumstances, always emerges in the summer, generally in July of the same year, as the summer form (var. *Napeæ*), yet out of these numerous pupæ I did not get a single butterfly during the year 1872. In winter I kept them in a warm room, and the first butterflies emerged in January, 1873, the remainder following in February, March, and April, and two females not until June. All appeared, however, as exquisite winter forms. The whole course of development was precisely as though cold had acted on the pupæ; and in fact, I could find no other cause for this quite exceptional deportment than the seven hours' shaking to which the pupæ were exposed by the railway journey, immediately after or during their transformation.

It is obviously a fact of fundamental importance to the theory of seasonal dimorphism, that the summer form can be readily changed into the winter form, whilst the latter cannot be changed into the summer form. I have thus far only made experiments on this subject with *A. Levana*, but the same fact appears to me to obtain for *P. Napi*. I did not, however, operate upon the ordinary winter form of *P. Napi*, but chose for this experiment the variety *Bryoniæ*, well known to all entomologists. This is, to a certain extent, the potential winter form of *P. Napi*; the male (Fig. 14, Plate I.) exactly resembles the ordinary winter form in the most minute detail, but the female is distinguished from *Napi* by a sprinkling of greyish brown scales over the whole of the upper side of the wings (Fig. 15, Plate I.). This type, *Bryoniæ*, occurs in Polar regions as the only form of *Napi*, and is also found in the higher Alps, where it flies in secluded meadows as the only form, but in other localities, less isolated, mixed with the ordinary form of the species. In both regions *Bryoniæ* produces but one generation in the year, and must thus, according to my theory, be regarded as the parent-form of *Pieris Napi*.

If this hypothesis is correct – if the variety *Bryoniæ* is really the original form preserved from the glacial period in certain regions of the earth, whilst *Napi* in its winter form is the first secondary form gradually produced through a warm climate, then it would be impossible ever to breed the ordinary form *Napi* from pupæ of *Bryoniæ* by the action of warmth, since the form of the species now predominant must have come into existence only by a cumulative action exerted on numerous generations, and not *per saltum*.

The experiment was made in the following manner: In the first part of June I caught a female of *Bryoniæ* in a secluded Alpine valley, and placed her in a capacious breeding-cage, where she flew about among the flowers, and laid more than a hundred eggs on the ordinary cabbage. Although the caterpillars in the free state feed upon another plant unknown to me, they readily ate the cabbage, grew rapidly, and pupated at the end of July. I then brought the pupæ into a hothouse in which the temperature fluctuated between 12° and 24° R.; but, in spite of this high temperature, and – what is certainly of more special importance – notwithstanding the want of cooling at night, only one butterfly emerged the same summer, and that a male, which, from certain minute characteristic markings, could be safely identified as var. *Bryoniæ*. The other pupæ hibernated in the heated room, and produced, from the end of January to the beginning of June, 28 butterflies, all of which were exquisite *Bryoniæ*.

Experiment thus confirmed the view that *Bryoniæ* is the parent-form of *Napi*, and the description hitherto given by systematists ought therefore properly to be reversed. *Pieris Bryoniæ* should be elevated to the rank of a species, and the ordinary winter and summer forms should be designated as vars. *Napi* and *Napeæ*. Still I should not like to take it upon myself to increase the endless confusion in the synonomy of butterflies. In a certain sense, it is also quite correct to describe the form

Bryoniæ as a climatic variety, for it is, in fact, established, if not produced, by climate, by which agency it is likewise preserved; only it is not a secondary, but the primary, climatic variety of *Napi*. In this sense most species might probably be described as climatic varieties, inasmuch as under the influence of another climate they would gradually acquire new characters, whilst, under the influence of the climate now prevailing in their habitats, they have, to a certain extent, acquired and preserved their present form.

The var. *Bryoniæ* is, however, of quite special interest, since it makes clear the relation which exists between climatic variation and seasonal dimorphism, as will be proved in the next section. The correctness of the present theory must first here be submitted to further proof.

It has been shown that the secondary forms of seasonally dimorphic butterflies do not all possess the tendency to revert in the same degree, but that this tendency rather varies with each individual. As the return to the primary form is synonymous with the relinquishing of the secondary, the greater tendency to revert is thus synonymous with the greater tendency to relinquish the secondary form, but this again is equivalent to a lesser stability of the latter; it must consequently be concluded that the individuals of a species are very differently influenced by climatic change, so that with some the new form must become sooner established than with others. From this a variability of the generation concerned must necessarily ensue, i.e., the individuals of the summer generation must differ more in colour and marking than is the case with those of the winter generation. If the theory is correct, the summer generations should be more variable than the winter generations – at least, so long as the greatest possible equalization of individual variations has not occurred through the continued action of warmth, combined with the constant crossing of individuals which have become changed in different degrees. Here also the theory is fully in accord with facts.

In *A. Levana* the *Levana* form is decidedly more constant than the *Prorsa* form. The first is, to a slight extent, sexually dimorphic, the female being light and the male dark-coloured. If we take into consideration this difference between the sexes, which also occurs to a still smaller extent in the *Prorsa* form, the foregoing statement will be found correct, viz. that the *Levana* form varies but little, and in all cases considerably less than the *Prorsa* form, in which the greatest differences occur in the yellow stripes and in the disappearance of the black spots on the white band of the hind wing, these black spots being persistent *Levana* markings. It is, in fact, difficult to find two perfectly similar individuals of the *Prorsa* form. It must, moreover, be considered that the *Levana* marking, being the more complicated, would the more readily show variation. Precisely the same thing occurs in *Pieris Napi*, in which also the var. *Æstiva* is considerably more variable than the var. *Vernalis*. From the behaviour of the var. *Bryoniæ*, on the other hand, which I regard as the parent-form, one might be tempted to raise an objection to the theory; for this form is well known to be extraordinarily variable in colour and marking, both in the Alps and Jura, where it is met with at the greatest altitudes. According to the theory, *Bryoniæ* should be less variable than the winter form of the lowlands, because it is the older, and should therefore be the more constant in its characters. It must not be forgotten, however, that the variability of a species may not only originate in the one familiar manner of unequal response of the individual to the action of varying exciting causes, but also by the crossing of two varieties separately established in adjacent districts and subsequently brought into contact. In the Alps and Jura the ordinary form of *Napi* swarms everywhere from the plains towards the habitats of *Bryoniæ*, so that a crossing of the two forms may occasionally, or even frequently, take place; and it is not astonishing if in some places (Meiringen, for example) a perfect series of intermediate forms between *Napi* and *Bryoniæ* is met with. That crossing is the cause of the great variability of *Bryoniæ* in the Alpine districts, is proved by the fact that in the Polar regions this form "is by no means so variable as in the Alps, but, judging from about forty to fifty Norwegian specimens, is rather constant." My friend, Dr. Staudinger, who has twice spent the summer in Lapland, thus writes in reply to my question. A crossing with *Napi* cannot there take place, as this form is never met with, so that the ancient parent-form *Bryoniæ* has been able to preserve its original constancy. In this case also the facts thus accord with the requirements of the theory.

II. Seasonal Dimorphism and Climatic Variation

If, as I have attempted to show, seasonal dimorphism originates through the slow operation of a changed summer climate, then is this phenomenon nothing else than the splitting up of a species into two climatic varieties in the same district, and we may expect to find various connexions between ordinary simple climatic variation and seasonal dimorphism. Cases indeed occur in which seasonal dimorphism and climatic variation pass into each other, and are interwoven in such a manner that the insight into the origin and nature of seasonal dimorphism gained experimentally finds confirmation. Before I go more closely into this subject, however, it is necessary to come to an understanding as to the conception "climatic variation," for this term is often very arbitrarily applied to quite dissimilar phenomena.

According to my view there should be a sharp distinction made between climatic and local varieties. The former should comprehend only such cases as originate through the direct action of climatic influences; while under the general designation of "local forms," should be comprised all variations which have their origin in other causes – such, for example, as in the indirect action of the external conditions of life, or in circumstances which do not owe their present existence to climate and external conditions, but rather to those geological changes which produce isolation. Thus, for instance, ancient species elsewhere long extinct might be preserved in certain parts of the earth by the protecting influence of isolation, whilst others which immigrated in a state of variability might become transformed into local varieties in such regions through the action of 'amixia,'[24] i.e. by not being allowed to cross with their companion forms existing in the other portions of their habitat. In single cases it may be difficult, or for the present impossible, to decide whether we have before us a climatic form, or a local form arising from other causes; but for this very reason we should be cautious in defining climatic variation.

The statement that climatic forms, in the true sense of the word, do exist is well known to me, and has been made unhesitatingly by all zoologists; indeed, a number of authentically observed facts might be produced, which prove that quite constant changes in a species may be brought about by the direct action of changed climatic conditions. With butterflies it is in many cases possible to separate pure climatic varieties from other local forms, inasmuch as we are dealing with only unimportant changes and not with those of biological value, so that natural selection may at the outset be excluded as the cause of the changes in question. Then again the sharply defined geographical distribution climatically governed, often furnishes

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[24] [The word 'Amixie,' from the Greek ἀμιξία, was first adopted by the author to express the idea of the prevention of crossing by isolation in his essay "Über den Einfluss der Isolirung auf die Artbildung," Leipzig, 1872, p. 49. R.M.]

evidence of transition forms in districts lying between two climatic extremes.

In the following attempt to make clear the relationship between simple climatic variation and seasonal dimorphism, I shall concern myself only with such undoubted climatic varieties. A case of this kind, in which the winter form of a seasonally dimorphic butterfly occurs in other habitats as the only form, i.e., as a climatic variety, has already been adduced in a former paragraph. I allude to the case of *Pieris Napi*, the winter form of which seasonally dimorphic species occurs in the temperate plains of Europe, whilst in Lapland and the Alps it is commonly found as a monomorphic climatic variety which is a higher development of the winter type, viz., the var. *Bryoniæ*.

Very analogous is the case of *Euchloe Belia*, a butterfly likewise belonging to the *Pierinæ*, which extends from the Mediterranean countries to the middle of France, and everywhere manifests a very sharply pronounced seasonal dimorphism. Its summer form was, until quite recently, described as a distinct species, *E. Ausonia*. Staudinger was the first to prove by breeding that the supposed two species were genetically related.[25] This species, in addition to being found in the countries named, occurs also at a little spot in the Alps in the neighbourhood of the Simplon Pass. Owing to the short summer of the Alpine climate the species has in this locality but one

[25] [Eng. ed. In 1844, Boisduval maintained this relationship of the two forms. See Speyer's "Geographische Verbreit. d. Schmetterl.," i. p. 455.]

annual brood, which bears the characters of the winter form, modified in all cases by the coarser thickly scattered hairs of the body (peculiar to many Alpine butterflies,) and some other slight differences. The var. *Simplonia* is thus in the Alps a simple climatic variety, whilst in the plains of Spain and the South of France it appears as the winter form of a seasonally dimorphic species.

This *Euchloe* var. *Simplonia* obviously corresponds to the var. *Bryoniæ* of *Pieris Napi*, and it is highly probable that this form of *E. Belia* must likewise be regarded as the parent-form of the species surviving from the glacial epoch, although it cannot be asserted, as can be done in the case of *Bryoniæ*, that the type has undergone no change since that epoch, for *Bryoniæ* from Lapland is identical with the Alpine form,[26] whilst *E. Simplonia* does not appear to occur in Polar countries.

Very interesting also is the case of *Polyommatus Phlæas*, Linn., one of our commonest *Lycænidæ*, which has a very wide distribution, extending from Lapland to Spain and Sicily.[27]

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[26] According to a written communication from Dr. Staudinger, the female *Bryoniæ* from Lapland are never so dusky as is commonly the case in the Alps, but they often have, on the other hand, a yellow instead of a white ground-colour. In the Alps, yellow specimens are not uncommon, and in the Jura are even the rule.

[27] [According to W. F. Kirby (Syn. Cat. Diurn. Lepidop.), the species is almost cosmopolitan, occurring, as well as throughout Europe, in Northern India (var. *Timeus*), Shanghai (var. *Chinensis*), Abyssinia (var. *Pseudophlæas*), Massachusetts (var. *Americana*), and California (var. *Hypophlæas*). In a long series from Northern India, in my own collection, all the specimens are extremely dark, the males being almost black. R.M.]

If we compare specimens of this beautiful copper-coloured butterfly from Lapland with those from Germany, no constant difference can be detected; the insect has, however, but one annual generation in Lapland, whilst in Germany it is double-brooded; but the winter and summer generations resemble each other completely, and specimens which had been caught in spring on the Ligurian coast were likewise similarly coloured to those from Sardinia. (Fig. 21, Plate II.). According to these facts we might believe this species to be extraordinarily indifferent to climatic influence; but the South European summer generation differs to a not inconsiderable extent from the winter generation just mentioned, the brilliant coppery lustre being nearly covered with a thick sprinkling of black scales. (Plate II., Fig. 22.) The species has thus become seasonally dimorphic under the influence of the warm southern climate, although this is not the case in Germany where it also has two generations in the year.[28] No one who is acquainted only with the Sardinian summer form, and not with the winter form of that place, would hesitate to regard the former as a climatic variety of our *P. Phlæas*; or, conversely, the north German form as a climatic variety of the southern summer form – according as he accepts the one or the other as the primary form of the species.

Still more complex are the conditions in another species of

[28] [Eng. ed. From a written communication from Dr. Speyer, it appears that also in Germany there is a small difference between the two generations. The German summer brood has likewise more black on the upper side, although seldom so much as the South European summer brood.]

Lycænidæ, *Plebeius Agestis* (= *Alexis* Scop.), which presents a double seasonal dimorphism. This butterfly appears in three forms; in Germany A and B alternate with each other as winter and summer forms, whilst in Italy B and C succeed each other as winter and summer forms. The form B thus occurs in both climates, appearing as the summer form in Germany and as the winter form in Italy. The German winter variety A, is entirely absent in Italy (as I know from numerous specimens which I have caught), whilst the Italian summer form, on the other hand, (var. *Allous*, Gerh.), does not occur in Germany. The distinctions between the three forms are sufficiently striking. The form A (Fig. 18, Plate II.) is blackish-brown on the upper side, and has in the most strongly marked specimens only a trace of narrow red spots round the borders; whilst the form B (Fig. 19, Plate II.) is ornamented with vivid red border spots; and C (Fig. 20, Plate II.) is distinguished from B by the strong yellowish-brown of the under side. If we had before us only the German winter and the Italian summer forms, we should, without doubt, regard them as climatic varieties; but they are connected by the form B, interpolated in the course of the development of both, and the two extremes thus maintain the character of mere seasonal forms.

III. Nature of the Causes producing Climatic Varieties

It has been shown that the phenomenon of seasonal dimorphism has the same proximate cause as climatic variation, viz. change of climate, and that it must be regarded as identical in nature with climatic variation, being distinguished from ordinary, or, as I have designated it, simple (monomorphic) climatic variation by the fact that, besides the new form produced by change of climate, the old form continues to exist in genetic connexion with it, so that old and new forms alternate with each other according to the season.

Two further questions now present themselves for investigation, viz. (1) by what means does change of climate induce a change in the marking and colouring of a butterfly? and (2) to what extent does the climatic action determine the nature of the change?

With regard to the former question, it must, in the first place, be decided whether the true effect of climatic change lies in the action of a high or low temperature on the organism, or whether it may not perhaps be produced by the accelerated development caused by a high temperature, and the retarded development caused by a low temperature. Other factors belonging to the category of external conditions of life which are included in the term “climate” may be disregarded, as they are of no importance in these cases. The question under consideration is difficult to decide, since, on the one hand, warmth and a short pupal period, and, on the other hand, cold and a long pupal period, are generally inseparably connected with each other; and without great caution one may easily be led into fallacies, by attributing to the influence of causes now acting that which is but the consequence of long inheritance.

When, in the case of *Araschnia Levana*, even in very cold summers, *Prorsa*, but never the *Levana* form, emerges, it would still be erroneous to conclude that it is only the shorter period of development of the winter generation, and not the summer warmth, which occasioned the formation of the *Prorsa* type. This new form of the species did not come suddenly into existence, but (as appears sufficiently from the foregoing experiments) originated in the course of many generations, during which summer warmth and a short development period were generally associated together. From the fact that the winter generation always produces *Levana*, even when the pupæ have not been exposed to cold but kept in a room, it would be equally erroneous to infer that the cold of winter had no influence in determining the type. In this case also the determining causes must have been in operation during innumerable generations. After the winter form of the species has become established throughout such a long period, it remains constant, even when the external influence which produced it (cold) is occasionally withdrawn.

Experiments cannot further assist us here, since we cannot observe throughout long periods of time; but there are certain observations, which to me appear decisive. When, both in Germany and Italy, we see *Polyommatus Phlæas* appearing in two generations, of which both the German ones are alike, whilst in Italy the summer brood is black, we cannot ascribe this fact to the influence of a shorter period of development, because this period is the same both in Germany and Italy (two annual generations), so that it can only be attributed to the higher temperature of summer.

Many similar cases might be adduced, but the one given suffices for proof. I am therefore of opinion that it is not the duration of the period of development which is the cause of change in the formation of climatic varieties of butterflies, but only the temperature to which the species is exposed during its pupal existence. In what manner, then, are we to conceive that warmth acts on the marking and colouring of a butterfly? This is a question which could only be completely answered by gaining an insight into the mysterious chemico-physiological processes by which the butterfly is formed in the chrysalis; and indeed only by such a complete insight into the most minute details, which are far beyond our scrutiny, could we arrive at, or even approximate to, an explanation of the development of any living organism. Nevertheless an important step can be taken towards the solution of this problem, by establishing that the change does not depend essentially upon the action of warmth, but upon the organism itself, as appears from the nature of the change in one and the same species.

If we compare the Italian summer form of *Polyommatus Phlæas* with its winter form, we shall find that the difference between them consists only in the brilliant coppery red colour of the latter being largely suffused in the summer form with black scales. When entomologists speak of a "black dusting" of the upper side of the wings, this statement must not of course be understood literally; the number of scales is the same in both forms, but in the summer variety they are mostly black, a comparatively small number being red. We might thus be inclined to infer that, owing to the high temperature, the chemistry of the material undergoing transformation in *Phlæas* is changed in such a manner that less red and more black pigment is produced. But the case is not so simple, as will appear evident when we consider the fact that the summer forms have not originated suddenly, but only in the course of numerous generations; and when we further compare the two seasonal forms in other species. Thus in *Pieris Napi* the winter is distinguished from the summer form, among other characters, by the strong black dusting of the base of the wings. But we cannot conclude from this that in the present case more black pigment is produced in the winter than in the summer form, for in the latter, although the base of the wings is white, their tips and the black spots on the fore-wings are larger and of a deeper black than in the winter form. The quantity of black pigment produced does not distinguish between the two forms, but the mode of its distribution upon the wings.

Even in the case of species the summer form of which really possesses far more black than the winter form, as, for instance, *Araschnia Levana*, one type cannot be derived from the other simply by the expansion of the black spots present, since on the same place where in *Levana* a black band crosses the wings, *Prorsa*, which otherwise possesses much more black, has a white line. (See Figs. 1–9, Plate I.) The intermediate forms which have been artificially produced by the action of cold on the summer generation present a graduated series, according as reversion is more or less complete; a black spot first appearing in the middle of the white band of *Prorsa*, and then becoming enlarged until, finally, in the perfect *Levana* it unites with another black triangle proceeding from the front of the band, and thus becomes fused into a black bar. The white band of *Prorsa* and the black band of *Levana* by no means correspond in position; in *Prorsa* quite a new pattern appears, which does not originate by a simple colour replacement of the *Levana* marking. In the present case, therefore, there is no doubt that the new form is not produced simply because a certain pigment (black) is formed in larger quantities, but because its mode of distribution is at the same time different, white appearing in some instances where black formerly existed, whilst in other cases the black remains. Whoever compares *Prorsa* with *Levana* will not fail to be struck with the remarkable change of marking produced by the direct action of external conditions.

The numerous intermediate forms which can be produced artificially appear to me to furnish a further proof of the gradual character of the transformation. Ancestral intermediate forms can only occur where they have once had a former existence in the phyletic series. Reversion may only take place completely in some particular characters, whilst in others the new form remains constant – this is in fact the ordinary form of reversion, and in this manner a mixture of characters might appear which never existed as a phyletic stage; but particular characters could certainly never appear unless they were normal to the species at some stage of phyletic development. Were this possible it would directly contradict the idea of reversion, according to which new characters never make their appearance, but only such as have already existed. If, therefore, the ancestral forms of *A. Levana* (which we designate as *Porima*) present a great number of transitional varieties, this leads to the conclusion that the species must have gone through a long series of stages of phyletic development before the summer generation had completely changed into *Prorsa*. The view of the slow cumulative action of climatic influences already submitted, is thus confirmed.

If warmth is thus without doubt the agency which has gradually changed the colour and marking of many of our butterflies, it sufficiently appears from what has just been said concerning the nature of the change that the chief part in the transmutation is not to be attributed to the agency in question, but to the organism which is affected by it. Induced by warmth, there begins a change in the ultimate processes of the matter undergoing transformation, which increases from generation to generation, and which not only consists in the appearance of the colouring matter in one place instead of another, but also in the replacement of yellow, in one place by white and in another by black, or in the transformation of black into white on some portions of the wings, whilst in others black remains. When we consider with what extreme fidelity the most insignificant details of marking are, in constant species of butterflies, transmitted from generation to generation, a total change of the kind under consideration cannot but appear surprising, and we should not explain it by the nature of the agency (warmth), but only by the nature of the species affected. The latter cannot react upon the warmth in the same manner that a solution of an iron salt reacts upon potassium ferrocyanide or upon sulphuretted hydrogen; the colouring matter of the butterfly's wing which was previously black does not become blue or yellow, nor does that which was white become changed into black, but a new marking is developed from the existing one – or, as I may express it in more general terms, the species takes another course of development; the complicated chemico-physical processes in the matter composing the pupa become gradually modified in such a manner that, as the final result, a new marking and colouring of the butterfly is produced.

Further facts can be adduced in support of the view that in these processes it is the constitution of the species, and not the external agency (warmth), which plays the chief part. The latter, as Darwin has strikingly expressed it, rather performs the function of the spark which ignites a combustible substance, whilst the character of the combustion depends upon the nature of the explosive material. Were this not the case, increased warmth would always change a given colour[29] in the same manner in all butterflies, and would therefore always give rise to the production of the same colour. But this does not occur; *Polyommatus Phlæas*, for example, becoming black in the south, whilst the red-brown *Vanessa Urticæ* becomes black in high northern latitudes, and many other cases well known to entomologists might be adduced.[30] It indeed appears that species of similar physical constitution, i.e., nearly allied species, under similar climatic influences, change in an analogous manner. A beautiful example of this is furnished by our *Pierinæ*. Most of the species display seasonal dimorphism; as, for instance,

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[29] [Assuming that in all butterflies similar colours are produced by the same chemical compounds. R.M.]

[30] [Mr. H. W. Bates mentions instances of local variation in colour affecting many distinct species in the same district in his memoir "On the Lepidoptera of the Amazon Valley;" Trans. Linn. Soc., vol. xxiii. Mr. A. R. Wallace also has brought together a large number of cases of variation in colour according to distribution, in his address to the biological section of the British Association at Glasgow in 1876. See "Brit. Assoc. Report," 1876, pp. 100–110. For observations on the change of colour in British Lepidoptera according to distribution see papers by Mr. E. Birchall in "Ent. Mo. Mag.," Nov., 1876, and by Dr. F. Buchanan White, "Ent. Mo. Mag.," Dec., 1876. The colour variations in all these cases are of course not *protective* as in the well-known case of *Gnophos obscurata*, &c. R.M.]

Pieris Brassicæ, *Rapæ*, *Napi*, *Krueperi*, and *Daplidice*, *Euchloe Belia* and *Belemia*, and *Leucophasia Sinapis*, in all of which the difference between the winter and the summer forms is of a precisely similar nature. The former are characterized by a strong black dusting of the base of the wings, and by a blackish or green sprinkling of scales on the underside of the hind wings, while the latter have intensely black tips to the wings, and frequently also spots on the fore-wings.

Nothing can prove more strikingly, however, that in such cases everything depends upon the physical constitution, than the fact that in the same species the males become changed in a different manner to the females. The parent-form of *Pieris Napi* (var. *Bryoniæ*) offers an example. In all the *Pierinæ* secondary sexual differences are found, the males being differently marked to the females; the species are thus sexually dimorphic. Now the male of the Alpine and Polar var. *Bryoniæ*, which I conceive to be the ancestral form, is scarcely to be distinguished, as has already been mentioned, from the male of our German winter form (*P. Napi*, var. *Vernalis*), whilst the female differs considerably.[31] The gradual climatic change which transformed the parent-form *Bryoniæ* into *Napi* has therefore exerted a much greater effect on the female than on the male. The external action on the two sexes was exactly the same, but the response of the organism was different, and the cause of the difference can only be sought for in the fine differences of physical constitution which distinguish

[31] See Figs. 10 and 14, 11 and 15, Plate I.

the male from the female. If we are unable to define these differences precisely, we may nevertheless safely conclude from such observations that they exist.

I have given special prominence to this subject because, in my idea, Darwin ascribes too much power to sexual selection when he attributes the formation of secondary sexual characters to the sole action of this agency. The case of *Bryoniæ* teaches us that such characters may arise from purely innate causes; and until experiments have decided how far the influence of sexual selection extends, we are justified in believing that the sexual dimorphism of butterflies is due in great part to the differences of physical constitution between the sexes. It is quite different with such sexual characters as the stridulating organs of male Orthoptera which are of undoubted importance to that sex. These can certainly be attributed with great probability to sexual selection.

It may perhaps not be superfluous to adduce one more similar case, in which, however, the male and not the female is the most affected by climate. In our latitudes, as also in the extreme north, *Polyommatus Phlæas*, already so often mentioned, is perfectly similar in both sexes in colour and marking; and the same holds good for the winter generation of the south. The summer generation of the latter, however, exhibits a slight sexual dimorphism, the red of the fore wings of the female being less completely covered with black than in the male.

IV. Why all Polygoneutic Species are not Seasonally Dimorphic

If we may consider it to be established that seasonal dimorphism is nothing else than the splitting up of a species into two climatic varieties in one and the same locality, the further question at once arises why all polygoneutic species (those which produce more than *one* annual generation) are not seasonally dimorphic.

To answer this, it will be necessary to go more deeply into the development of seasonal dimorphism. This evidently depends upon a peculiar kind of periodic, alternating heredity, which we might be tempted to identify with Darwin's "inheritance at corresponding periods of life." It does not, however, in any way completely agree with this principle, although it presents a great analogy to it and must depend ultimately upon the same cause. The Darwinian "inheritance at corresponding periods of life" – or, as it is termed by Haeckel, "homochronic heredity" – is characterized by the fact that new characters always appear in the individuals at the same stage of life as that in which they appeared in their progenitors. The truth of this principle has been firmly established, instances being known in which both the first appearance of a new (especially pathological) character and its transmission through several generations has been observed. Seasonally dimorphic butterflies also furnish a further valuable proof of this principle, since they show that not only variations which arise suddenly (and which are therefore probably due to purely innate causes) follow this mode of inheritance, but also that characters gradually called forth by the influence of external conditions and accumulating from generation to generation, are only inherited at that period of life in which these conditions were or are effective. In all seasonally dimorphic butterflies which I have been able to examine closely, I found the caterpillars of the summer and winter broods to be perfectly identical. The influences which, by acting on the pupæ, split up the imagines into two climatic forms, were thus without effect on the earlier stages of development. I may specially mention that the caterpillars, as well as the pupæ and eggs of *A. Levana*, are perfectly alike both in the summer and winter forms; and the same is the case in the corresponding stages of *P. Napi* and *P. Bryoniæ*.

I shall not here attempt to enter more deeply into the nature of the phenomena of inheritance. It is sufficient to have confirmed the law that influences which act only on certain stages in the development of the individual, even when the action is cumulative and not sudden, only affect those particular stages without having any effect on the earlier or later stages. This law is obviously of the greatest importance to the comprehension of metamorphosis. Lubbock[32] has briefly shown in a very clear manner how the existence of metamorphosis in insects can

[32] "On the Origin and Metamorphoses of Insects," London, 1874.

be explained by the indirect action of varying conditions on the different life-stages of a species. Thus the mandibles of a caterpillar are, by adaptation to another mode of nourishment, exchanged at a later period of life for a suctorial organ. Such adaptation of the various development-stages of a species to the different conditions of life would never give rise to metamorphosis, if the law of homochronic, or periodic, heredity did not cause the characters gradually acquired at a given stage to be transferred to the same stage of the following generation.

The origin of seasonal dimorphism depends upon a very similar law, or rather form, of inheritance, which differs from that above considered only in the fact that, instead of the ontogenetic stages, a whole series of generations is influenced. This form of inheritance may be formulated somewhat as follows: – When dissimilar conditions alternatingly influence a series of generations, a cycle is produced in which the changes are transmitted only to those generations which are acted upon by corresponding conditions, and not to the intermediate ones. Characters which have arisen by the action of a summer climate are inherited by the summer generation only, whilst they remain latent in the winter generation. It is the same as with the mandibles of a caterpillar which are latent in the butterfly, and again make their appearance in the corresponding (larval) stage of the succeeding generation. This is not mere hypothesis, but the legitimate inference from the facts. If it be admitted that my conception of seasonal dimorphism as a double climatic variation is correct, the law of "cyclical heredity,"[33] as I may term it – in contradistinction to "homochronic heredity," which relates only to the ontogenetic stages – immediately follows. All those cases which come under the designation of 'alternation of generation,' can obviously be referred to cyclical heredity, as will be explained further on. In the one case the successive generations deport themselves exactly in the same manner as do the successive stages of development of the individual in the other; and we may conclude therefrom (as has long been admitted on other grounds) that a generation is, in fact, nothing else than a stage of development in the life of a species. This appears to me to furnish a beautiful confirmation of the theory of descent.

Now if, returning to questions previously solved, the alternating action of cold in winter and warmth in summer leads to the production of a winter and summer form, according to the law of cyclical heredity, the question still remains: why do we not find seasonal dimorphism in all polygoneutic butterflies?

We might at first suppose that all species are not equally sensitive to the influence of temperature: indeed, the various amounts of difference between the winter and summer forms

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[33] I at first thought of designating the two forms of cyclical or homochronic heredity as ontogenetic- and phyletic-cyclical heredity. The former would certainly be correct; the latter would be also applicable to alternation of generation (in which actually two or more phyletic stages alternate with each other) but not to all those cases which I attribute to heterogenesis, in which, as with seasonal dimorphism, a series of generations of *the same* phyletic stage constitute the point of departure.

in different species would certainly show the existence of different degrees of sensitiveness to the modifying action of temperature. But even this does not furnish an explanation, since there are butterflies which produce two perfectly similar[34] generations wherever they occur, and which, nevertheless, appear in different climates as climatic varieties. This is the case with *Pararga Ægeria* (Fig. 23, Plate II.), the southern variety of which, *Meione* (Fig. 24, Plate II.), is connected with it by an intermediate form from the Ligurian coast. This species possesses, therefore, a decided power of responding to the influence of temperature, and yet no distinction has taken place between the summer and the winter form. We can thus only attribute this different deportment to a different kind of heredity; and we may therefore plainly state, that changes produced by alternation of climate are not always inherited *alternatingly*, i.e. by the corresponding generations, but sometimes *continuously*, appearing in every generation, and never remaining latent. The causes which determine why, in a particular case, the one or the other form of inheritance prevails, can be only innate, i.e. they lie in the organism itself, and there is as little to be said upon their precise nature as upon that of any other process of heredity. In a

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[34] When Meyer-Dürr, who is otherwise very accurate, states in his "Verzeichniss der Schmetterlinge der Schweiz," (1852, p. 207), that the winter and summer generations of *P. Ægeria* differ to a small extent in the contour of the wings and in marking, he has committed an error. The characters which this author attributes to the summer form are much more applicable to the female sex. There exists in this species a trifling sexual dimorphism, but no seasonal dimorphism.

similar manner Darwin admits a kind of double inheritance with respect to characters produced by sexual selection; in one form these characters remain limited to the sex which first acquired them, in the other form they are inherited by both sexes, without it being apparent why, in any particular case, the one or the other form of heredity should take place.

The foregoing explanation may obtain in the case of sexual selection, in which it is not inconceivable that certain characters may not be so easily produced, or even not produced at all, in one sex, owing to its differing from the other in physical constitution. In the class of cases under consideration, however, it is not possible that the inherited characters can be prevented from being acquired by one generation owing to its physical constitution, since this constitution was similar in all the successive generations before the appearance of dimorphism. The constitution in question first became dissimilar in the two generations to the extent of producing a change of specific character, through the action of temperature on the alternating broods of each year, combined with cyclical heredity. If the law of cyclical heredity be a general one, it must hold good for all cases, and characters acquired by the summer generation could never have been also transmitted to the winter generation from the very first.

I will not deny the possibility that if alternating heredity should become subsequently entirely suppressed throughout numerous generations, a period may arrive when the preponderating influence of a long series of summer generations may ultimately take effect upon the winter generation. In such a case the summer characters would appear, instead of remaining latent as formerly. In this manner it may be imagined that at first but few, and later more numerous individuals, approximate to the summer form, until finally the dimorphism entirely disappears, the new form thus gaining ascendency and the species becoming once more monomorphic. Such a supposition is indeed capable of being supported by some facts, an observation on *A. Levana* apparently contradicting the theory having been already interpreted in this sense. I refer to the fact that whilst some butterflies of the winter generation emerge in October as *Prorsa*, others hibernate, and appear the following spring in the *Levana* form. The winter form of *Pieris Napi* also no longer preserves, in the female sex, the striking coloration of the ancestral form *Bryoniæ*, a fact which may indicate the influencing of the winter generation by numerous summer generations. The double form of the spring generation of *Papilio Ajax* can be similarly explained by the gradual change of alternating into continuous heredity, as has already been mentioned. All these cases, however, are perhaps capable of another interpretation; at any rate, the correctness of this supposition can only be decided by further facts.

Meanwhile, even if we suppose the above explanation to be correct, it will not apply to the absence of seasonal dimorphism in cases like that of *Pararga Ægeria* and *Meione*, in which only *one* summer generation appears, so that a preponderating inheritance of summer characters cannot be admitted. Another explanation must thus be sought, and I believe that I have found it in the circumstance that the butterflies named do not hibernate as pupæ but as caterpillars, so that the cold of winter does not directly influence those processes of development by which the perfect insect is formed in the chrysalis. It is precisely on this point that the origin of those differences of colour which we designate as the seasonal dimorphism of butterflies appears to depend. Previous experiments give great probability to this statement. From these we know that the eggs, caterpillars, and pupæ of all the seasonally dimorphic species experimented with are perfectly similar in the summer and winter generations, the imago stage only showing any difference. We know further from these experiments, that temperature-influences which affect the caterpillars never entail a change in the butterflies; and finally, that the artificial production of the reversion of the summer to the winter form can only be brought about by operating on the pupæ.

Since many monogoneutic species now hibernate in the caterpillar stage (e.g. *Satyrus Proserpina*, and *Hermione*, *Epinephele Eudora*, *Furtina, Ithonus*, *Hyperanthus*, *Ida*, *&c.*), we may admit that during the glacial period such species did not pass the winter as pupæ. As the climate grew warmer, and in consequence thereof a second generation became gradually interpolated in many of these monogoneutic species, there would ensue (though by no means necessarily) a disturbance of the winter generation, of such a kind that the pupæ, instead of the caterpillars as formerly, would then hibernate. It may, indeed, be easily proved *à priori* that whenever a disturbance of the winter generation takes place it only does so retrogressively, that is to say – species which at one time pass the winter as caterpillars subsequently hibernate in the egg, while those which formerly hibernate as pupæ afterwards do so as caterpillars. The interpolation of a summer generation must necessarily delay till further towards the end of summer, the brood about to hibernate; the remainder of the summer, which serves for the development of the eggs and young caterpillars, may possibly under these conditions be insufficient for pupation, and the species which hibernated in the pupal state when it was monogoneutic, may perhaps pass the winter in the larval condition after the introduction of the second brood. A disturbance of this kind is conceivable; but it is certain that many species suffer no further alteration in their development than that of becoming digoneutic from monogoneutic. This follows from the fact that hibernation takes place in the caterpillar stage in many species of the sub-family *Satyridæ* which are now digoneutic, as well as in the remaining monogoneutic species of the same sub-family. But we cannot expect seasonal dimorphism to appear in all digoneutic butterflies the winter generation of which hibernates in the caterpillar form, since the pupal stage in these species experiences nearly the same influences of temperature in both generations. We are hence led to the conclusion that seasonal dimorphism must arise in butterflies whenever the pupæ of the alternating annual generations are exposed throughout long periods of time to widely different regularly recurring changes of temperature.

The facts agree with this conclusion, inasmuch as most butterflies which exhibit seasonal dimorphism hibernate in the pupa stage. Thus, this is the case with all the *Pierinæ*, with *Papilio Machaon*, *P. Podalirius*, and *P. Ajax*, as well as with *Araschnia Levana*. Nevertheless, it cannot be denied that seasonal dimorphism occurs also in some species which do not hibernate as pupæ but as caterpillars; as, for instance, in the strongly dimorphic *Plebeius Amyntas*. But such cases can be explained in a different manner.

Again, the formation of a climatic variety – and as such must we regard seasonally dimorphic forms – by no means entirely depends on the magnitude of the difference between the temperature which acts on the pupæ of the primary and that which acts on those of the secondary form; it rather depends on the absolute temperature which the pupæ experience. This follows without doubt from the fact that many species, such as our common Swallow-tail (*Papilio Machaon*), and also *P. Podalirius*, in Germany and the rest of temperate Europe, show no perceptible difference of colour between the first generation, the pupæ of which hibernate, and the second generation, the pupal period of which falls in July, whereas the same butterflies in South Spain and Italy are to a small extent seasonally dimorphic. Those butterflies which are developed under the influence of a Sicilian summer heat likewise show climatic variation to a small extent. The following consideration throws further light on these conditions. The mean summer and winter temperatures in Germany differ by about 14.9° R.; this difference being therefore much more pronounced than that between the German and Sicilian summer, which is only about 3.6° R. Nevertheless, the winter and summer generations of *P. Podalirius* are alike in Germany, whilst the Sicilian summer generation has become a climatic variety. The cause of this change must therefore lie in the small difference between the mean summer temperatures of 15.0° R. (Berlin) and 19.4° R. (Palermo). According to this, a given absolute temperature appears to give a tendency to variation in a certain direction, the necessary temperature being different for different species. The latter statement is supported by the facts that, in the first place, in different species there are very different degrees of difference between the summer and winter forms; and secondly, many digoneutic species are still monomorphic in Germany, first becoming seasonally dimorphic in Southern Europe. This is the case with *P. Machaon* and *P. Podalirius*, as already mentioned, and likewise with *Polyommatus Phlæas*. Zeller in 1846–47, during his journey in Italy, recognized as seasonally dimorphic in a small degree a large number of diurnal Lepidoptera which are not so in our climate.[35]

In a similar manner the appearance of seasonal dimorphism in species which, like *Plebeius Amyntas*, do not hibernate as pupæ, but as caterpillars, can be simply explained by supposing that the winter generation was the primary form, and that the increase in the summer temperature since the glacial period was sufficient to cause this particular species to become changed by the gradual interpolation of a second generation. The dimorphism of *P. Amyntas* can, nevertheless, be explained in another manner. Thus, there may have been a disturbance of the period of development in the manner already indicated, the species which formerly hibernated in the pupal stage becoming subsequently disturbed in its course of development by the interpolation of a summer generation, and hibernating in consequence in the caterpillar state. Under these circumstances we must regard the present winter form (var. *Polysperchon*) as having been established under the influence of a winter climate, this form, since the supposed disturbance in its development, having had no reason to become changed, the spring temperature under which its pupation now takes place not being sufficiently high. The interpolated second generation on the other hand, the pupal period of which falls in the height of summer, may easily have become formed into a summer variety.

This latter explanation agrees precisely with the former, both

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[35] P. C. Zeller, "Bemerkungen über die auf einer Reise nach Italien und Sicilien gesammelten Schmetterlingsarten." Isis, 1847, ii. – xii.

starting with the assumption that in the present case, as in that of *A. Levana* and the *Pierinæ*, the winter form is the primary one, so that the dimorphism proceeds from the said winter form and does not originate the winter but the summer form, as will be explained. Whether the winter form has been produced by the action of the winter or spring temperature is immaterial in judging single cases, inasmuch as we are not in a position to state what temperature is necessary to cause any particular species to become transformed.

The reverse case is also theoretically conceivable, viz., that in certain species the summer form was the primary one, and by spreading northwards a climate was reached which still permitted the production of two generations, the pupal stage of one generation being exposed to the cold of winter, and thus giving rise to the production of a secondary winter form. In such a case hibernation in the pupal state would certainly give rise to seasonal dimorphism. Whether these conditions actually occur, appears to me extremely doubtful; but it may at least be confidently asserted that the first case is of far more frequent occurrence. The beautiful researches of Ernst Hoffmann[36] furnish strong evidence for believing that the great majority of the European butterflies have immigrated, not from the south, but from Siberia. Of 281 species, 173 have, according to Hoffmann, come from Siberia, 39 from southern Asia, and only 8 from Africa, whilst during the greatest cold of the glacial period, but very few or possibly no

[36] "Isoporien der europäischen Tagfalter." Stuttgart, 1873.

species existed north of the Alps. Most of the butterflies now found in Europe have thus, since their immigration, experienced a gradually increasing warmth. Since seasonal dimorphism has been developed in some of these species, the summer form must in all cases have been the secondary one, as the experiments upon the reversion of *Pieris Napi* and *Araschnia Levana* have also shown.

All the seasonally dimorphic butterflies known to me are found in Hoffmann's list of Siberian immigrants, with the exception of two species, viz., *Euchloe Belemia*, which is cited as an African immigrant, and *Pieris Krueperi*, which may have come through Asia Minor, since at the present time it has not advanced farther west than Greece. No considerable change of climate can be experienced by migrating from east to west, so that the seasonal dimorphism of *Pieris Krueperi* can only depend on a cause similar to that which affected the Siberian immigrants, that is, the gradual increase of temperature in the northern hemisphere since the glacial period. In this species also, the winter form must be the primary one. In the case of *E. Belemia*, on the other hand, the migration northwards from Africa certainly indicates removal to a cooler climate, which may have originated a secondary winter form, even if nothing more certain can be stated. We know nothing of the period of migration into southern Europe; and even migration without climatic change is conceivable, if it kept pace with the gradual increase of warmth in the northern hemisphere since the glacial epoch. Experiments only would in this case be decisive. If the summer generation, var. *Glauce*, were the primary form, it would not be possible by the action of cold on the pupæ of this brood to produce the winter variety *Belemia*, whilst, on the other hand, the pupæ of the winter generation by the influence of warmth would be made to revert more or less completely to the form *Glauce*. It is by no means to be understood that the species would actually comport itself in this manner. On the contrary, I am of opinion that in this case also, the winter form is primary. The northward migration (from Africa to south Spain) would be quite insufficient, and the winter form is now found in Africa as well as in Spain.

V. On Alternation of Generations

Seasonal dimorphism has already been designated by Wallace as alternation of generation,[37] a term which cannot be disputed so long as it is confined to a regular alternation of dissimilar generations. But little is gained by this definition, however, unless it can be proved that both phenomena are due to similar causes, and that they are consequently brought about by analogous processes. The causes of alternation of generation have, until the present time, been scarcely investigated, owing to the want of material. Haeckel alone has quite recently subjected these complicated phenomena generally to a searching investigation, and has arrived at the conclusion that the various forms of metagenesis can be arranged in two series. He distinguishes a progressive and a retrogressive series, comprising under the former those species "which, to a certain extent, are still in a transition stage from monogenesis to amphigenesis (asexual to sexual propagation), and the early progenitors of which, therefore, never exclusively propagated themselves sexually" (*Trematoda*, *Hydromedusæ*). Under the other, or retrogressive form of metagenesis, Haeckel includes a "return from amphigenesis to monogenesis," this being the case with all those species which now manifest a regular alternation from amphigenesis to parthenogenesis (*Aphides*, *Rotatoria*,

[37] [Trans. Linn. Soc., vol. xxv. 1865, p. 9. R.M.]

Daphniidæ, *Phyllopoda*, &c.). Essentially I can but agree entirely with Haeckel. Simply regarding the phenomena of alternation of generation as at present known, it appears to me to be readily admissible that these multiform modes of propagation must have originated in at least two different ways, which can be aptly formulated in the manner suggested by Haeckel.

I will, however, venture to adopt a somewhat different mode of conception, and regard the manner of propagation (whether sexual or asexual) not as the determining, but only as the secondary cause. I will further hazard the separation of the phenomena of alternating generations (in their widest sense) into two main groups according to their origin, designating the cases of one group as true metagenesis and those of the other as heterogenesis.[38] Metagenesis takes its origin from a phyletic series of dissimilar forms, whilst heterogenesis originates from a phyletic series of similar forms – this series, so far as we can at present judge, always consisting of similar sexual generations. The former would thus nearly coincide with Haeckel's progressive, and the latter with his retrogressive metagenesis. Metagenesis may further originate in various ways. In the first place, from metamorphosis, as for example, in the propagation of the celebrated *Cecidomyia* with nursing larvæ.

[38] It is certainly preferable to make use of the expression "metagenesis" in this special sense instead of introducing a new one. As a general designation, comprehending metagenesis and heterogenesis, there will then remain the expression "alternation of generation," if one does not prefer to say "cyclical propagation." The latter may be well used in contradistinction to "metamorphosis."

The power which these larvæ possess of propagating themselves asexually has evidently been acquired as a secondary character, as appears from the fact that there are many species of the same genus the larvæ of which do not nurse, these larvæ being themselves undoubted secondary forms produced by the adaptation of this stage of phyletic development to a mode of life widely different from that of the later stages. In the form now possessed by these larvæ they could never have represented the final stage of their ontogeny, neither could they have formerly possessed the power of sexual propagation. The conclusion seems inevitable that metagenesis has here proceeded from metamorphosis; that is to say, one stage of the ontogeny, by acquiring asexual propagation, has changed the originally existing metamorphosis into metagenesis.

Lubbock[39] is undoubtedly correct when, for cases like that just mentioned, he attempts to derive alternation of generations from metamorphosis. But if we exclude heterogenesis there still remain a large number of cases of true metagenesis which cannot be explained from this point of view.

It must be admitted, with Haeckel, that the alternation of generations in the Hydromedusæ and Trematoda does not depend, as in the case of *Cecidomyia*, upon the larvæ having acquired the power of nursing, but that the inferior stages of these species always possessed this power which they now only preserve. The nursing Trematode larvæ now existing may

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[39] *Loc. cit.* chap. iv.

possibly have been formerly able to propagate themselves also sexually, this mode of propagation having at the present time been transferred to a later phyletic stage. In this case, therefore, metagenesis was not properly produced by metamorphosis, but arose therefrom in the course of the phyletic development, the earlier phyletic stages abandoning the power of sexual reproduction, and preserving the asexual mode of propagation. A third way in which metagenesis might originate is through polymorphosis. When the latter is combined with asexual reproduction, as is especially the case with the Hydrozoa, metagenesis may be derived therefrom. The successive stages of transformation of one and the same physiological individual do not in these cases serve as the point of departure for alternation of generation, but the different contemporary forms living gregariously into which the species has become divided through functional differentiation of the various individuals of the same stock. Individuals are here produced which alone acquire the power of sexual reproduction, and metagenesis is thus brought about, these individuals detaching themselves from the stock on which they originated, while the rest of the individuals remain in combination, and retain the asexual mode of propagation. No sharp distinction can be otherwise drawn between this and the cases previously considered.[40] The difference consists only in the

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[40] The idea that alternation of generation is derived from polymorphism (not the reverse, as usually happens; i.e. polymorphism from alternation of generation) is not new, as I find whilst correcting the final proof. Semper has already expressed it at the conclusion of his interesting memoir, "Über Generationswechsel bei Steinkorallen,"

whole cycle of reproduction being performed by one stock; both classes have the common character that the different phyletic stages never appear in the same individual (metamorphosis), but in the course of further phyletic development metagenesis at the same time arises, i.e. the division of these stages among a succession of individuals. We are therefore able to distinguish this *primary metagenesis* from the *secondary metagenesis* arising from metamorphosis.

It is not here my intention to enter into the ultimate causes of metagenesis; in this subject we should only be able to advance by making vague hypotheses. The phenomenon of seasonal dimorphism, with which this work has mainly to deal, is evidently far removed from metagenesis, and it was to make this clear that the foregoing observations were brought forward. The characters common in the origin of metagenesis are to be found, according to the views previously set forth, in the facts that here the faculty of asexual and of sexual reproduction is always distributed among *several* phyletic stages of development which succeed each other in an ascending series (progressive metagenesis of Haeckel), whereas I find differences only in the fact that the power of asexual propagation may (in metagenesis) be either newly acquired (larva of *Cecidomyia*) or preserved from previous ages (*Hydroida*). It seems that in this process sexual reproduction is without exception lost by the earlier, and remains confined solely to the most recent stages.

&c. See "Zeitschrift f. wiss. Zool." vol. xxii. 1872.

From the investigations on seasonal dimorphism it appears that a cycle of generations can arise in an entirely different way. In this case a series of generations originally alike are made dissimilar by external influences. This appears to me of the greatest importance, since seasonal dimorphism is without doubt closely related to that mode of reproduction which has hitherto been exclusively designated as heterogenesis, and a knowledge of its mode of origination must therefore throw light on the nature and origin of heterogenesis in general.

In seasonal dimorphism, as I have attempted to show, it is the direct action of climate, and indeed chiefly that of temperature, which brings about the change in some of the generations. Since these generations have been exposed to the alternating influence of the summer and winter temperature a periodical dimorphism has been developed – a regular cycle of dissimilar generations. It has already been asserted that the consecutive generations of a species comport themselves with respect to heredity in a manner precisely similar to that of the ontogenetic stages, and at the same time such succeeding generations point out the parallelism between metamorphosis and heterogenesis. If influences capable of directly or indirectly producing changes operate on any particular stage of development, these changes are always transmitted to the same stage. Upon this metamorphosis depends. In a precisely similar manner changes which operated periodically on certain generations (1, 3, 5, for instance) are transmitted to these generations only, and not to the intermediate ones. Upon this depends heterogenesis. We have just been led to the comprehension of heterogenesis by cyclical heredity, by the fact that a cycle is produced whenever a series of generations exists under regularly alternating influences. In this cycle newly acquired changes, however minute in character at first, are only transmitted to a later, and not to the succeeding generation, appearing only in the one corresponding, i.e. in that generation which exists under similar transforming influences. Nothing can more clearly show the extreme importance which the conditions of life must have upon the formation and further development of species than this fact. At the same time nothing shows better that the action of these conditions is not suddenly and violently exerted, but that it rather takes place by small and slow operations. In these cases the long-continued accumulation of imperceptibly small variations proves to be the magic means by which the forms of the organic world are so powerfully moulded. By the application of even the greatest warmth nobody would be able to change the winter form of *A. Levana* into the summer form; nevertheless, the summer warmth, acting regularly on the second and third generations of the year, has, in the course of a lengthened period, stamped these two generations with a new form without the first generation being thereby changed. In the same region two different climatic varieties have been produced (just as in the majority of cases climatic varieties occur only in separate regions) which alternate with each other, and thus give rise to a cycle of which each generation propagates itself sexually.

But even if seasonal dimorphism is to be ascribed to heterogenesis, it must by no means be asserted that those cases of cyclical propagation hitherto designated as heterogenesis are completely identical with seasonal dimorphism. Their identity extends only to their origin and manner of development, but not to the mode of operation of the causes which bring about their transformation. Both phenomena have a common mode of origination, arising from similar (monomorphic) sexual generations and course of development, a cycle of generations with gradually diverging characters coming into existence by the action of alternating influences. On the other hand, the nature of the changes by which the secondary differs from the primary generation may be referred to another mode of action of the exciting causes. In seasonal dimorphism the differences between the two generations are much less than in other cases of heterogenesis. These differences are both quantitatively less, and are likewise qualitative, affecting only characters of biological insignificance.[41] The variations in question are mostly restricted to the marking and colouring of the wings and body, occasionally affecting also the form of the wing, and in a few cases the size of the body (*Plebeius Amyntas*), whilst the bodily structure – so far at least as my investigations extend – appears to be the same in both generations.[42]

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[41] See my essay "Über den Einfluss der Isolirung auf die Artbildung." Leipzig, 1872.

[42] [In the case of monogoneutic species which, by artificial 'forcing,' have been made to give two generations in the year, it has generally been found that the reproductive

The state of affairs is quite different in the remaining cases of heterogenesis; here the entire structure of the body appears to be more or less changed, and its size is often very different, nearly all the internal organs differing in the two generations. According to Claus,[43] "we can scarcely find any other explanation of the mode of origination of heterogenesis than the gradual and slow advantageous adaptation of the organization to important varying conditions of life" – a judgment in which this author is certainly correct. In all such cases the change does not affect unimportant characters, as it does in butterflies, but parts of biological or physiological value; and we cannot, therefore, consider such changes to have originated through the *direct* action of altered conditions of life, but *indirectly* through natural selection or adaptation.

Thus, the difference between seasonal dimorphism and the other known cases of heterogenesis consists in the secondary form in which the species appears in the former originating through the direct action of external conditions, whilst in the latter this form most probably originates through the indirect action of such influences. The first half of the foregoing proposition is alone capable of provisional proof, but it is in the highest degree probable that the latter half is also correct. Naturally we cannot say to what extent the direct action of

system has been imperfectly developed in the second brood. A minute anatomical investigation of the sexual organs in the two broods of seasonally dimorphic insects would be of great interest, and might lead to important results. R.M.]

[43] "Grundzüge der Zoologie." 2nd ed. Leipzig, 1872. Introduction.

external conditions plays also a part in true heterogenesis, as there have been as yet no experiments made on its origin. That direct action, working to a certain extent co-operatively, plays only a secondary part, while the chief cause of the change is to be found in adaptation, no one can doubt who keeps in view, for instance, the mode of propagation discovered by Leuckart in *Ascaris nigrovenosa*. In this worm, the one generation lives free in the water, and the other generation inhabits the lungs of frogs, the two generations differing from one another in size of body and structure of internal organs to an extent only possible with the true Nematoda.

To prevent possible misunderstanding, let it be finally noted – even if superfluous – that the changes causing the diversity of the two generations in seasonal dimorphism and heterogenesis are not of such a nature that the value of different "specific characters" can be attached to them. Distinctly defined specific characters are well known not to occur generally, and it would therefore be erroneous to attach but little value to the differences in seasonal dimorphism because these chiefly consist in the colouring and marking of the wings. The question here under consideration is not whether two animal forms have the value of species or of mere varieties – a question which can never be decided, since the reply always depends upon individual opinion of the value of the distinctions in question, and the idea of both species and varieties is moreover purely conventional. The question is, rather, whether the distinguishing characters possess an equal constancy – that is, whether they are transmitted with the same force and accuracy to all individuals; and whether they occur, therefore, in such a manner that they can be practically employed as specific characters. With respect to this, it cannot be doubtful for a moment that the colouring and marking of a butterfly possess exactly the same value as the constant characters in any other group of animals, such as the palate-folds in mice, the structure of the teeth in mammals, the number and form of the wing and tail feathers in birds, &c. We have but to remember with what wonderful constancy often the most minute details of marking are transmitted in butterflies. The systematist frequently distinguishes between two nearly allied species, as for instance in the *Lycænidæ*

Конец ознакомительного фрагмента.