

**Contributions to the theory of natural selection a series of essays / by
Alfred Russel Wallace ...**

Contributors

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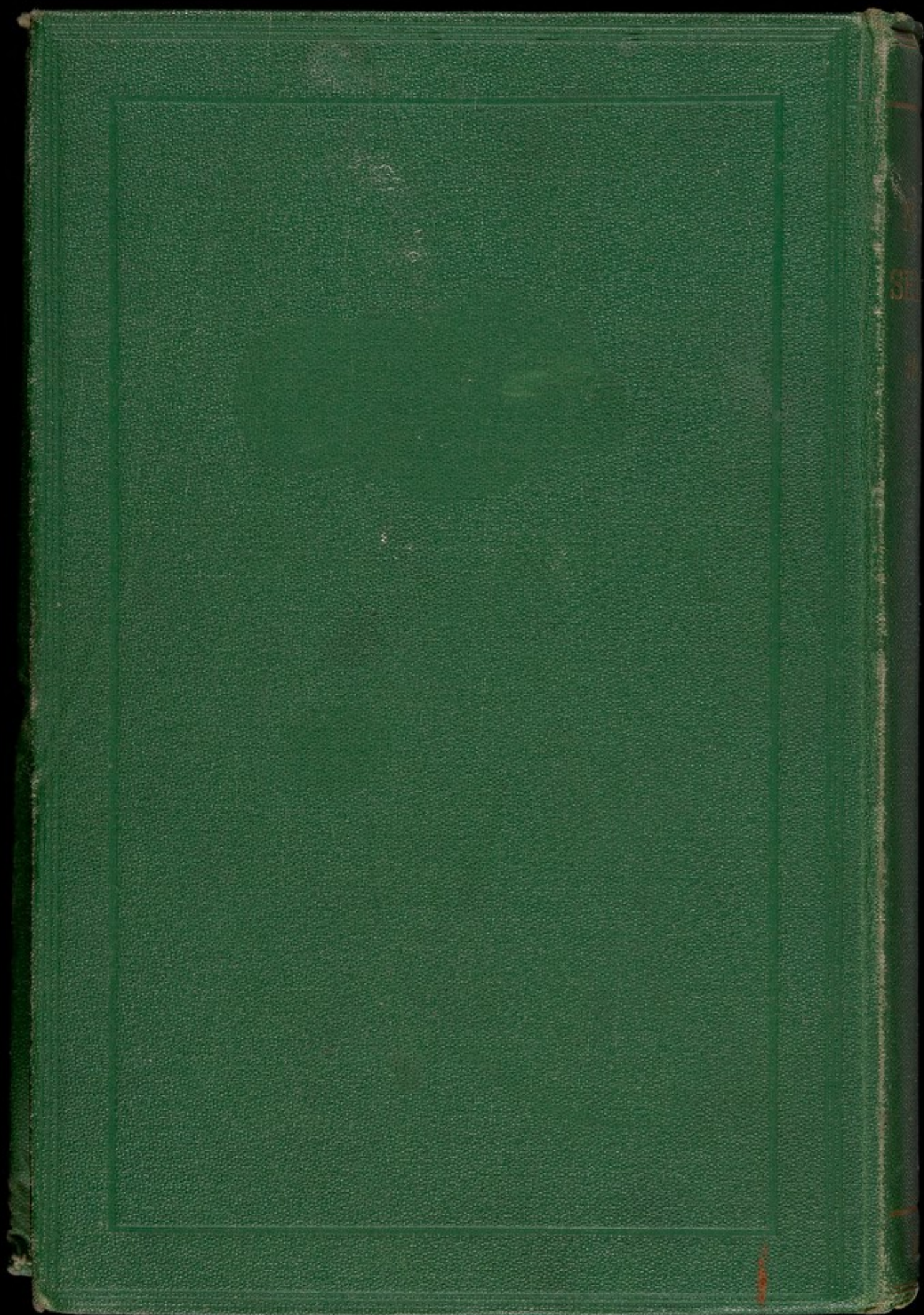
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CONTRIBUTIONS TO
THE THEORY OF
NATURAL SELECTION.

A Series of Essays.

BY
ALFRED RUSSEL WALLACE,
AUTHOR OF
"THE MALAY ARCHIPELAGO," ETC., ETC.

London:
MACMILLAN AND CO.,
1870.

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PREFACE.

THE present volume consists of essays which I have contributed to various periodicals, or read before scientific societies during the last fifteen years, with others now printed for the first time. The two first of the series are printed without alteration, because, having gained me the reputation of being an independent originator of the theory of "natural selection," they may be considered to have some historical value. I have added to them one or two very short explanatory notes, and have given headings to subjects, to make them uniform with the rest of the book. The other essays have been carefully corrected, often considerably enlarged, and in some cases almost rewritten, so as to express more fully and more clearly the views which I hold at the present time; and as most of them originally appeared in publications which have a very limited circulation, I believe that the larger portion of this volume will be new to many of my friends and to most of my readers.

I now wish to say a few words on the reasons which have led me to publish this work. The second essay, especially when taken in connection with the first, contains an outline sketch of the theory of the origin of species (by means of what was afterwards termed by Mr. Darwin—"natural selection,") as conceived

by me before I had the least notion of the scope and nature of Mr. Darwin's labours. They were published in a way not likely to attract the attention of any but working naturalists, and I feel sure that many who have heard of them, have never had the opportunity of ascertaining how much or how little they really contain. It therefore happens, that, while some writers give me more credit than I deserve, others may very naturally class me with Dr. Wells and Mr. Patrick Matthew, who, as Mr. Darwin has shown in the historical sketch given in the 4th and 5th Editions of the "Origin of Species," certainly propounded the fundamental principle of "natural selection" before himself, but who made no further use of that principle, and failed to see its wide and immensely important applications.

The present work will, I venture to think, prove, that I both saw at the time the value and scope of the law which I had discovered, and have since been able to apply it to some purpose in a few original lines of investigation. But here my claims cease. I have felt all my life, and I still feel, the most sincere satisfaction that Mr. Darwin had been at work long before me, and that it was not left for me to attempt to write "The Origin of Species." I have long since measured my own strength, and know well that it would be quite unequal to that task. Far abler men than myself may confess, that they have not that untiring patience in accumulating, and that wonderful skill in using, large masses of facts of the

most varied kind,—that wide and accurate physiological knowledge,—that acuteness in devising and skill in carrying out experiments,—and that admirable style of composition, at once clear, persuasive and judicial,—qualities, which in their harmonious combination mark out Mr. Darwin as the man, perhaps of all men now living, best fitted for the great work he has undertaken and accomplished.

My own more limited powers have, it is true, enabled me now and then to seize on some conspicuous group of unappropriated facts, and to search out some generalization which might bring them under the reign of known law; but they are not suited to that more scientific and more laborious process of elaborate induction, which in Mr. Darwin's hands has led to such brilliant results.

Another reason which has led me to publish this volume at the present time is, that there are some important points on which I differ from Mr. Darwin, and I wish to put my opinions on record in an easily accessible form, before the publication of his new work, (already announced,) in which I believe most of these disputed questions will be fully discussed.

I will now give the date and mode of publication of each of the essays in this volume, as well as the amount of alteration they have undergone.

I.—ON THE LAW WHICH HAS REGULATED THE INTRODUCTION OF NEW SPECIES.

First published in the "Annals and Magazine of

Natural History," September, 1855. Reprinted without alteration of the text.

II.—ON THE TENDENCY OF VARIETIES TO DEPART
INDEFINITELY FROM THE ORIGINAL TYPE.

First published in the "Journal of the Proceedings of the Linnæan Society," August, 1858. Reprinted without alteration of the text, except one or two grammatical emendations.

III.—MIMICRY AND OTHER PROTECTIVE RESEMBLANCES
AMONG ANIMALS.

First published in the "Westminster Review," July, 1867. Reprinted with a few corrections and some important additions, among which I may especially mention Mr. Jenner Weir's observations and experiments on the colours of the caterpillars eaten or rejected by birds.

IV.—THE MALAYAN PAPILIONIDÆ, OR SWALLOW-
TAILED BUTTERFLIES, AS ILLUSTRATIVE OF THE
THEORY OF NATURAL SELECTION.

First published in the "Transactions of the Linnæan Society," Vol. XXV. (read March, 1864), under the title, "On the Phenomena of Variation and Geographical Distribution, as illustrated by the Papilionidæ of the Malayan Region."

The introductory part of this essay is now reprinted, omitting tables, references to plates, &c., with some additions, and several corrections. Owing to the publi-

cation of Dr. Felder's "Voyage of the Novara" (Lepidoptera) in the interval between the reading of my paper and its publication, several of my new species must have their names changed for those given to them by Dr. Felder, and this will explain the want of agreement in some cases between the names used in this volume and those of the original paper.

V.—ON INSTINCT IN MAN AND ANIMALS.

Not previously published.

VI.—THE PHILOSOPHY OF BIRDS' NESTS.

First published in the "Intellectual Observer," July, 1867. Reprinted with considerable emendations and additions.

VII.—A THEORY OF BIRDS' NESTS ;

SHOWING THE RELATION OF CERTAIN DIFFERENCES OF COLOUR IN BIRDS TO THEIR MODE OF NIDIFICATION.

First published in the "Journal of Travel and Natural History" (No. 2), 1868. Now reprinted with considerable emendations and additions, by which I have endeavoured more clearly to express, and more fully to illustrate, my meaning in those parts which have been misunderstood by my critics.

VIII.—CREATION BY LAW.

First published in the "Quarterly Journal of Science," October, 1867. Now reprinted with a few alterations and additions.

IX.—THE DEVELOPMENT OF HUMAN RACES UNDER
THE LAW OF NATURAL SELECTION.

First published in the "Anthropological Review," May, 1864. Now reprinted with a few important alterations and additions. I had intended to have considerably extended this essay, but on attempting it I found that I should probably weaken the effect without adding much to the argument. I have therefore preferred to leave it as it was first written, with the exception of a few ill-considered passages which never fully expressed my meaning. As it now stands, I believe it contains the enunciation of an important truth.

X.—THE LIMITS OF NATURAL SELECTION AS APPLIED
TO MAN.

This is the further development of a few sentences at the end of an article on "Geological Time and the Origin of Species," which appeared in the "Quarterly Review," for April, 1869. I have here ventured to touch on a class of problems which are usually considered to be beyond the boundaries of science, but which, I believe, will one day be brought within her domain.

For the convenience of those who are acquainted with any of my essays in their original form, I subjoin references to the more important additions and alterations now made to them.

ADDITIONS AND CORRECTIONS TO THE ESSAYS AS
ORIGINALLY PUBLISHED.

Essays I. and II. are unaltered, but short notes are added at pp. 19, 24, 29, and 40.

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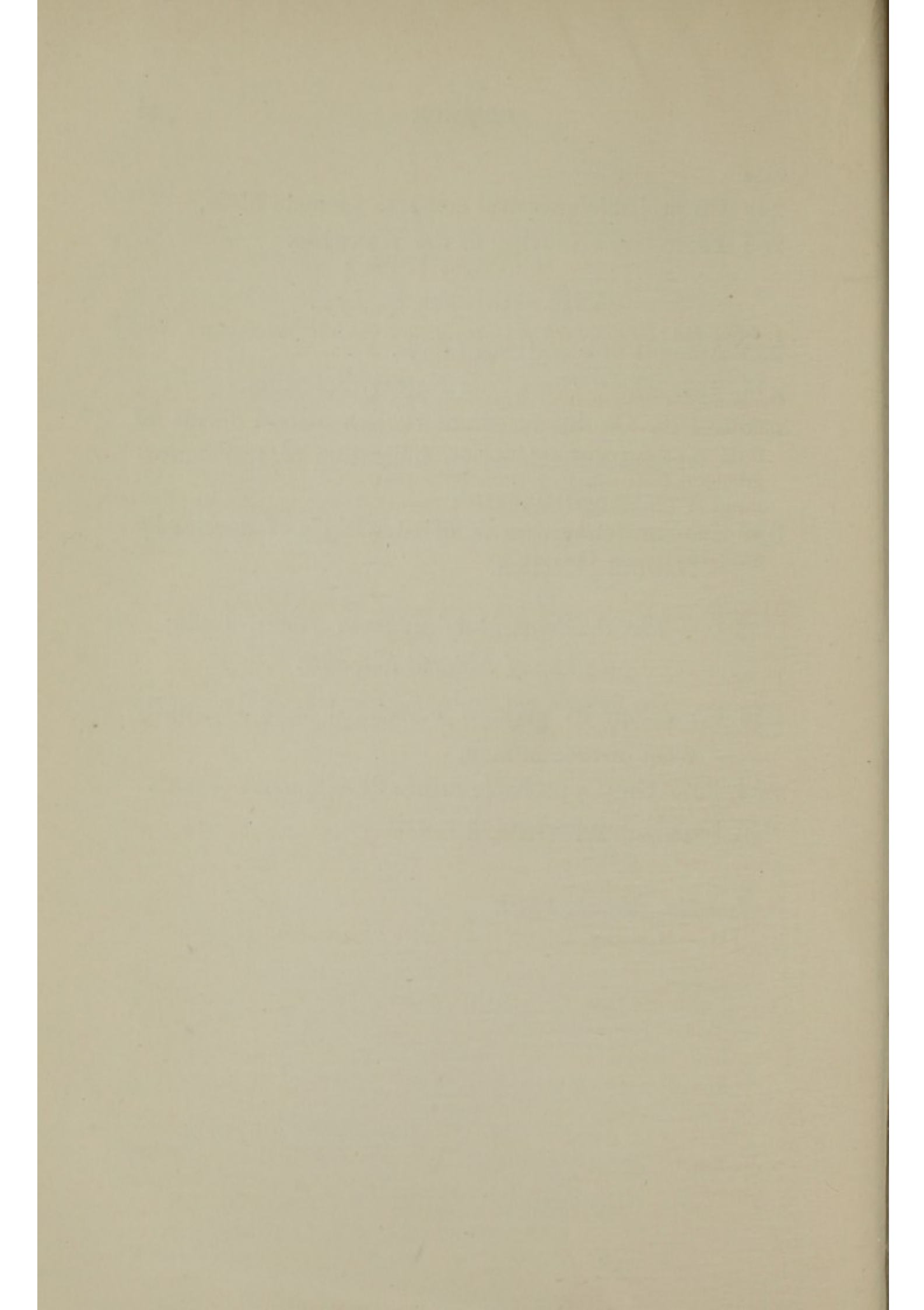
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London, March, 1870.



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I.

ON THE LAW WHICH HAS REGULATED THE INTRODUCTION OF NEW SPECIES.*

Geographical Distribution dependent on Geologic Changes.

75 EVERY naturalist who has directed his attention to the subject of the geographical distribution of animals and plants, must have been interested in the singular facts which it presents. Many of these facts are quite different from what would have been anticipated, and have hitherto been considered as highly curious, but quite inexplicable. None of the explanations attempted from the time of Linnæus are now considered at all satisfactory; none of them have given a cause sufficient to account for the facts known at the time, or comprehensive enough to include all the new facts which have since been, and are daily being added. Of late years, however, a great light has been thrown upon the subject by geological investigations, which have shown that the present state of the earth and of the organisms now

* Written at Sarawak in February, 1855, and published in the "Annals and Magazine of Natural History," September, 1855.

inhabiting it, is but the last stage of a long and uninterrupted series of changes which it has undergone, and consequently, that to endeavour to explain and account for its present condition without any reference to those changes (as has frequently been done) must lead to very imperfect and erroneous conclusions.

The facts proved by geology are briefly these:—That during an immense, but unknown period, the surface of the earth has undergone successive changes; land has sunk beneath the ocean, while fresh land has risen up from it; mountain chains have been elevated; islands have been formed into continents, and continents submerged till they have become islands; and these changes have taken place, not once merely, but perhaps hundreds, perhaps thousands of times:—That all these operations have been more or less continuous, but unequal in their progress, and during the whole series the organic life of the earth has undergone a corresponding alteration. This alteration also has been gradual, but complete; after a certain interval not a single species existing which had lived at the commencement of the period. This complete renewal of the forms of life also appears to have occurred several times:—That from the last of the geological epochs to the present or historical epoch, the change of organic life has been gradual: the first appearance of animals now existing can in many cases be traced, their numbers gradually increasing in the more re-

cent formations, while other species continually die out and disappear, so that the present condition of the organic world is clearly derived by a natural process of gradual extinction and creation of species from that of the latest geological periods. We may therefore safely infer a like gradation and natural sequence from one geological epoch to another.

Now, taking this as a fair statement of the results of geological inquiry, we see that the present geographical distribution of life upon the earth must be the result of all the previous changes, both of the surface of the earth itself and of its inhabitants. Many causes, no doubt, have operated of which we must ever remain in ignorance, and we may, therefore, expect to find many details very difficult of explanation, and in attempting to give one, must allow ourselves to call into our service geological changes which it is highly probable may have occurred, though we have no direct evidence of their individual operation.

The great increase of our knowledge within the last twenty years, both of the present and past history of the organic world, has accumulated a body of facts which should afford a sufficient foundation for a comprehensive law embracing and explaining them all, and giving a direction to new researches. It is about ten years since the idea of such a law suggested itself to the writer of this essay, and he has since taken every opportunity of testing it by all the newly-ascertained facts with which he has become

acquainted, or has been able to observe himself. These have all served to convince him of the correctness of his hypothesis. Fully to enter into such a subject would occupy much space; and it is only in consequence of some views having been lately promulgated, he believes, in a wrong direction, that he now ventures to present his ideas to the public, with only such obvious illustrations of the arguments and results as occur to him in a place far removed from all means of reference and exact information.

A Law deduced from well-known Geographical and Geological Facts.

The following propositions in Organic Geography and Geology give the main facts on which the hypothesis is founded.

Geography.

1. Large groups, such as classes and orders, are generally spread over the whole earth, while smaller ones, such as families and genera, are frequently confined to one portion, often to a very limited district.

2. In widely distributed families the genera are often limited in range; in widely distributed genera, well marked groups of species are peculiar to each geographical district.

3. When a group is confined to one district, and is rich in species, it is almost invariably the case that the most closely allied species are found in the same locality or in closely adjoining localities, and

that therefore the natural sequence of the species by affinity is also geographical.

4. In countries of a similar climate, but separated by a wide sea or lofty mountains, the families, genera and species of the one are often represented by closely allied families, genera and species peculiar to the other.

Geology.

5. The distribution of the organic world in time is very similar to its present distribution in space.

6. Most of the larger and some small groups extend through several geological periods.

7. In each period, however, there are peculiar groups, found nowhere else, and extending through one or several formations.

8. Species of one genus, or genera of one family occurring in the same geological time are more closely allied than those separated in time.

9. As generally in geography no species or genus occurs in two very distant localities without being also found in intermediate places, so in geology the life of a species or genus has not been interrupted. In other words, no group or species has come into existence twice.

10. The following law may be deduced from these facts :—*Every species has come into existence coincident both in space and time with a pre-existing closely allied species.*

This law agrees with, explains and illustrates all the facts connected with the following branches of

the subject:—1st. The system of natural affinities. 2nd. The distribution of animals and plants in space. 3rd. The same in time, including all the phænomena of representative groups, and those which Professor Forbes supposed to manifest polarity. 4th. The phænomena of rudimentary organs. We will briefly endeavour to show its bearing upon each of these.

The Form of a true system of Classification determined by this Law.

If the law above enunciated be true, it follows that the natural series of affinities will also represent the order in which the several species came into existence, each one having had for its immediate antitype a closely allied species existing at the time of its origin. It is evidently possible that two or three distinct species may have had a common antitype, and that each of these may again have become the antitypes from which other closely allied species were created. The effect of this would be, that so long as each species has had but one new species formed on its model, the line of affinities will be simple, and may be represented by placing the several species in direct succession in a straight line. But if two or more species have been independently formed on the plan of a common antitype, then the series of affinities will be compound, and can only be represented by a forked or many branched line. Now, all attempts at a Natural classification and arrangement

of organic beings show, that both these plans have obtained in creation. Sometimes the series of affinities can be well represented for a space by a direct progression from species to species or from group to group, but it is generally found impossible so to continue. There constantly occur two or more modifications of an organ or modifications of two distinct organs, leading us on to two distinct series of species, which at length differ so much from each other as to form distinct genera or families. These are the parallel series or representative groups of naturalists, and they often occur in different countries, or are found fossil in different formations. They are said to have an analogy to each other when they are so far removed from their common antitype as to differ in many important points of structure, while they still preserve a family resemblance. We thus see how difficult it is to determine in every case whether a given relation is an analogy or an affinity, for it is evident that as we go back along the parallel or divergent series, towards the common antitype, the analogy which existed between the two groups becomes an affinity. We are also made aware of the difficulty of arriving at a true classification, even in a small and perfect group;—in the actual state of nature it is almost impossible, the species being so numerous and the modifications of form and structure so varied, arising probably from the immense number of species which have served as antitypes for the existing species, and thus produced a complicated branching of

the lines of affinity, as intricate as the twigs of a gnarled oak or the vascular system of the human body. Again, if we consider that we have only fragments of this vast system, the stem and main branches being represented by extinct species of which we have no knowledge, while a vast mass of limbs and boughs and minute twigs and scattered leaves is what we have to place in order, and determine the true position each originally occupied with regard to the others, the whole difficulty of the true Natural System of classification becomes apparent to us.

We shall thus find ourselves obliged to reject all those systems of classification which arrange species or groups in circles, as well as those which fix a definite number for the divisions of each group. The latter class have been very generally rejected by naturalists, as contrary to nature, notwithstanding the ability with which they have been advocated; but the circular system of affinities seems to have obtained a deeper hold, many eminent naturalists having to some extent adopted it. We have, however, never been able to find a case in which the circle has been closed by a direct and close affinity. In most cases a palpable analogy has been substituted, in others the affinity is very obscure or altogether doubtful. The complicated branching of the lines of affinities in extensive groups must also afford great facilities for giving a show of probability to any such purely artificial arrangements. Their death-blow

was given by the admirable paper of the lamented Mr. Strickland, published in the "Annals of Natural History," in which he so clearly showed the true synthetical method of discovering the Natural System.

Geographical Distribution of Organisms.

If we now consider the geographical distribution of animals and plants upon the earth, we shall find all the facts beautifully in accordance with, and readily explained by, the present hypothesis. A country having species, genera, and whole families peculiar to it, will be the necessary result of its having been isolated for a long period, sufficient for many series of species to have been created on the type of pre-existing ones, which, as well as many of the earlier-formed species, have become extinct, and thus made the groups appear isolated. If in any case the antitype had an extensive range, two or more groups of species might have been formed, each varying from it in a different manner, and thus producing several representative or analogous groups. The Sylviadæ of Europe and the Sylvicolidæ of North America, the Heliconidæ of South America and the Euplœas of the East, the group of Trogons inhabiting Asia, and that peculiar to South America, are examples that may be accounted for in this manner.

Such phænomena as are exhibited by the Gala-

pagos Islands, which contain little groups of plants and animals peculiar to themselves, but most nearly allied to those of South America, have not hitherto received any, even a conjectural explanation. The Galapagos are a volcanic group of high antiquity, and have probably never been more closely connected with the continent than they are at present. They must have been first peopled, like other newly-formed islands, by the action of winds and currents, and at a period sufficiently remote to have had the original species die out, and the modified prototypes only remain. In the same way we can account for the separate islands having each their peculiar species, either on the supposition that the same original emigration peopled the whole of the islands with the same species from which differently modified prototypes were created, or that the islands were successively peopled from each other, but that new species have been created in each on the plan of the pre-existing ones. St. Helena is a similar case of a very ancient island having obtained an entirely peculiar, though limited, flora. On the other hand, no example is known of an island which can be proved geologically to be of very recent origin (late in the Tertiary, for instance), and yet possesses generic or family groups, or even many species peculiar to itself.

When a range of mountains has attained a great elevation, and has so remained during a long geological period, the species of the two sides at and

near their bases will be often very different, representative species of some genera occurring, and even whole genera being peculiar to one side only, as is remarkably seen in the case of the Andes and Rocky Mountains. A similar phenomenon occurs when an island has been separated from a continent at a very early period. The shallow sea between the Peninsula of Malacca, Java, Sumatra and Borneo was probably a continent or large island at an early epoch, and may have become submerged as the volcanic ranges of Java and Sumatra were elevated. The organic results we see in the very considerable number of species of animals common to some or all of these countries, while at the same time a number of closely allied representative species exist peculiar to each, showing that a considerable period has elapsed since their separation. The facts of geographical distribution and of geology may thus mutually explain each other in doubtful cases, should the principles here advocated be clearly established.

In all those cases in which an island has been separated from a continent, or raised by volcanic or coralline action from the sea, or in which a mountain-chain has been elevated in a recent geological epoch, the phenomena of peculiar groups or even of single representative species will not exist. Our own island is an example of this, its separation from the continent being geologically very recent, and we have consequently scarcely a species which is peculiar to it; while the Alpine range, one of the most

recent mountain elevations, separates faunas and floras which scarcely differ more than may be due to climate and latitude alone.

The series of facts alluded to in Proposition (3), of closely allied species in rich groups being found geographically near each other, is most striking and important. Mr. Lovell Reeve has well exemplified it in his able and interesting paper on the Distribution of the Bulimi. It is also seen in the Humming-birds and Toucans, little groups of two or three closely allied species being often found in the same or closely adjoining districts, as we have had the good fortune of personally verifying. Fishes give evidence of a similar kind: each great river has its peculiar genera, and in more extensive genera its groups of closely allied species. But it is the same throughout Nature; every class and order of animals will contribute similar facts. Hitherto no attempt has been made to explain these singular phænomena, or to show how they have arisen. Why are the genera of Palms and of Orchids in almost every case confined to one hemisphere? Why are the closely allied species of brown-backed Trogons all found in the East, and the green-backed in the West? Why are the Macaws and the Cockatoos similarly restricted? Insects furnish a countless number of analogous examples;—the Goliathi of Africa, the Ornithopteræ of the Indian Islands, the Heliconidæ of South America, the Danaidæ of the East, and in all, the most closely allied species found

in geographical proximity. The question forces itself upon every thinking mind,—why are these things so? They could not be as they are had no law regulated their creation and dispersion. The law here enunciated not merely explains, but necessitates the facts we see to exist, while the vast and long-continued geological changes of the earth readily account for the exceptions and apparent discrepancies that here and there occur. The writer's object in putting forward his views in the present imperfect manner is to submit them to the test of other minds, and to be made aware of all the facts supposed to be inconsistent with them. As his hypothesis is one which claims acceptance solely as explaining and connecting facts which exist in nature, he expects facts alone to be brought to disprove it, not *à priori* arguments against its probability.

Geological Distribution of the Forms of Life.

The phænomena of geological distribution are exactly analogous to those of geography. Closely allied species are found associated in the same beds, and the change from species to species appears to have been as gradual in time as in space. Geology, however, furnishes us with positive proof of the extinction and production of species, though it does not inform us how either has taken place. The extinction of species, however, offers but little difficulty, and the *modus operandi* has been well illustrated by Sir

C. Lyell in his admirable "Principles." Geological changes, however gradual, must occasionally have modified external conditions to such an extent as to have rendered the existence of certain species impossible. The extinction would in most cases be effected by a gradual dying-out, but in some instances there might have been a sudden destruction of a species of limited range. To discover how the extinct species have from time to time been replaced by new ones down to the very latest geological period, is the most difficult, and at the same time the most interesting problem in the natural history of the earth. The present inquiry, which seeks to eliminate from known facts a law which has determined, to a certain degree, what species could and did appear at a given epoch, may, it is hoped, be considered as one step in the right direction towards a complete solution of it.

High Organization of very ancient Animals consistent with this Law.

Much discussion has of late years taken place on the question, whether the succession of life upon the globe has been from a lower to a higher degree of organization. The admitted facts seem to show that there has been a general, but not a detailed progression. Mollusca and Radiata existed before Vertebrata, and the progression from Fishes to Reptiles and Mammalia, and also from the lower mammals to the higher, is indisputable. On the other hand,

it is said that the Mollusca and Radiata of the very earliest periods were more highly organized than the great mass of those now existing, and that the very first fishes that have been discovered are by no means the lowest organised of the class. Now it is believed the present hypothesis will harmonize with all these facts, and in a great measure serve to explain them ; for though it may appear to some readers essentially a theory of progression, it is in reality only one of gradual change. It is, however, by no means difficult to show that a real progression in the scale of organization is perfectly consistent with all the appearances, and even with apparent retrogression, should such occur.

Returning to the analogy of a branching tree, as the best mode of representing the natural arrangement of species and their successive creation, let us suppose that at an early geological epoch any group (say a class of the Mollusca) has attained to a great richness of species and a high organization. Now let this great branch of allied species, by geological mutations, be completely or partially destroyed. Subsequently a new branch springs from the same trunk, that is to say, new species are successively created, having for their antitypes the same lower organized species which had served as the antitypes for the former group, but which have survived the modified conditions which destroyed it. This new group being subject to these altered conditions, has modifications of structure and organization given

to it, and becomes the representative group of the former one in another geological formation. It may, however, happen, that though later in time, the new series of species may never attain to so high a degree of organization as those preceding it, but in its turn become extinct, and give place to yet another modification from the same root, which may be of higher or lower organization, more or less numerous in species, and more or less varied in form and structure than either of those which preceded it. Again, each of these groups may not have become totally extinct, but may have left a few species, the modified prototypes of which have existed in each succeeding period, a faint memorial of their former grandeur and luxuriance. Thus every case of apparent retrogression may be in reality a progress, though an interrupted one: when some monarch of the forest loses a limb, it may be replaced by a feeble and sickly substitute. The foregoing remarks appear to apply to the case of the Mollusca, which, at a very early period, had reached a high organization and a great development of forms and species in the testaceous Cephalopoda. In each succeeding age modified species and genera replaced the former ones which had become extinct, and as we approach the present æra, but few and small representatives of the group remain, while the Gasteropods and Bivalves have acquired an immense preponderance. In the long series of changes the earth has undergone, the process of peopling it with organic beings has

been continually going on, and whenever any of the higher groups have become nearly or quite extinct, the lower forms which have better resisted the modified physical conditions have served as the antitypes on which to found the new races. In this manner alone, it is believed, can the representative groups at successive periods, and the risings and fallings in the scale of organization, be in every case explained.

Objections to Forbes' Theory of Polarity.

The hypothesis of polarity, recently put forward by Professor Edward Forbes to account for the abundance of generic forms at a very early period and at present, while in the intermediate epochs there is a gradual diminution and impoverishment, till the minimum occurred at the confines of the Palæozoic and Secondary epochs, appears to us quite unnecessary, as the facts may be readily accounted for on the principles already laid down. Between the Palæozoic and Neozoic periods of Professor Forbes, there is scarcely a species in common, and the greater part of the genera and families also disappear to be replaced by new ones. It is almost universally admitted that such a change in the organic world must have occupied a vast period of time. Of this interval we have no record; probably because the whole area of the early formations now exposed to our researches was elevated at the end of the Palæozoic period, and remained so through the interval required for the organic changes which

resulted in the fauna and flora of the Secondary period. The records of this interval are buried beneath the ocean which covers three-fourths of the globe. Now it appears highly probable that a long period of quiescence or stability in the physical conditions of a district would be most favourable to the existence of organic life in the greatest abundance, both as regards individuals and also as to variety of species and generic group, just as we now find that the places best adapted to the rapid growth and increase of individuals also contain the greatest profusion of species and the greatest variety of forms,—the tropics in comparison with the temperate and arctic regions. On the other hand, it seems no less probable that a change in the physical conditions of a district, even small in amount if rapid, or even gradual if to a great amount, would be highly unfavourable to the existence of individuals, might cause the extinction of many species, and would probably be equally unfavourable to the creation of new ones. In this too we may find an analogy with the present state of our earth, for it has been shown to be the violent extremes and rapid changes of physical conditions, rather than the actual mean state in the temperate and frigid zones, which renders them less prolific than the tropical regions, as exemplified by the great distance beyond the tropics to which tropical forms penetrate when the climate is equable, and also by the richness in species and forms of tropical mountain regions which principally

differ from the temperate zone in the uniformity of their climate. However this may be, it seems a fair assumption that during a period of geological repose the new species which we know to have been created would have appeared, that the creations would then exceed in number the extinctions, and therefore the number of species would increase. In a period of geological activity, on the other hand, it seems probable that the extinctions might exceed the creations, and the number of species consequently diminish. That such effects did take place in connexion with the causes to which we have imputed them, is shown in the case of the Coal formation, the faults and contortions of which show a period of great activity and violent convulsions, and it is in the formation immediately succeeding this that the poverty of forms of life is most apparent. We have then only to suppose a long period of somewhat similar action during the vast unknown interval at the termination of the Palæozoic period, and then a decreasing violence or rapidity through the Secondary period, to allow for the gradual repopulation of the earth with varied forms, and the whole of the facts are explained.* We thus have a clue to the increase of the forms of life during certain periods, and their decrease during others, without recourse

* Professor Ramsay has since shown that a glacial epoch probably occurred at the time of the Permian formation, which will more satisfactorily account for the comparative poverty of species.

to any causes but those we know to have existed, and to effects fairly deducible from them. The precise manner in which the geological changes of the early formations were effected is so extremely obscure, that when we can explain important facts by a retardation at one time and an acceleration at another of a process which we know from its nature and from observation to have been unequal,—a cause so simple may surely be preferred to one so obscure and hypothetical as polarity.

I would also venture to suggest some reasons against the very nature of the theory of Professor Forbes. Our knowledge of the organic world during any geological epoch is necessarily very imperfect. Looking at the vast numbers of species and groups that have been discovered by geologists, this may be doubted; but we should compare their numbers not merely with those that now exist upon the earth, but with a far larger amount. We have no reason for believing that the number of species on the earth at any former period was much less than at present; at all events the aquatic portion, with which geologists have most acquaintance, was probably often as great or greater. Now we know that there have been many complete changes of species; new sets of organisms have many times been introduced in place of old ones which have become extinct, so that the total amount which have existed on the earth from the earliest geological period must have borne about the same proportion to those now

living, as the whole human race who have lived and died upon the earth, to the population at the present time. Again, at each epoch, the whole earth was no doubt, as now, more or less the theatre of life, and as the successive generations of each species died, their exuviæ and preservable parts would be deposited over every portion of the then existing seas and oceans, which we have reason for supposing to have been more, rather than less, extensive than at present. In order then to understand our possible knowledge of the early world and its inhabitants, we must compare, not the area of the whole field of our geological researches with the earth's surface, but the area of the examined portion of each formation separately with the whole earth. For example, during the Silurian period all the earth was Silurian, and animals were living and dying, and depositing their remains more or less over the whole area of the globe, and they were probably (the species at least) nearly as varied in different latitudes and longitudes as at present. What proportion do the Silurian districts bear to the whole surface of the globe, land and sea (for far more extensive Silurian districts probably exist beneath the ocean than above it), and what portion of the known Silurian districts has been actually examined for fossils? Would the area of rock actually laid open to the eye be the thousandth or the ten-thousandth part of the earth's surface? Ask the same question with regard to the Oolite or the Chalk, or even to particular beds of these when

they differ considerably in their fossils, and you may then get some notion of how small a portion of the whole we know.

But yet more important is the probability, nay almost the certainty, that whole formations containing the records of vast geological periods are entirely buried beneath the ocean, and for ever beyond our reach. Most of the gaps in the geological series may thus be filled up, and vast numbers of unknown and unimaginable animals, which might help to elucidate the affinities of the numerous isolated groups which are a perpetual puzzle to the zoologist, may there be buried, till future revolutions may raise them in their turn above the waters, to afford materials for the study of whatever race of intelligent beings may then have succeeded us. These considerations must lead us to the conclusion, that our knowledge of the whole series of the former inhabitants of the earth is necessarily most imperfect and fragmentary,—as much so as our knowledge of the present organic world would be, were we forced to make our collections and observations only in spots equally limited in area and in number with those actually laid open for the collection of fossils. Now, the hypothesis of Professor Forbes is essentially one that assumes to a great extent the completeness of our knowledge of the whole series of organic beings which have existed on the earth. This appears to be a fatal objection to it, independently of all other considerations. It may be said that the same ob-

jections exist against every theory on such a subject, but this is not necessarily the case. The hypothesis put forward in this paper depends in no degree upon the completeness of our knowledge of the former condition of the organic world, but takes what facts we have as fragments of a vast whole, and deduces from them something of the nature and proportions of that whole which we can never know in detail. It is founded upon isolated groups of facts, recognizes their isolation, and endeavours to deduce from them the nature of the intervening portions.

Rudimentary Organs

Another important series of facts, quite in accordance with, and even necessary deductions from, the law now developed, are those of rudimentary organs. That these really do exist, and in most cases have no special function in the animal œconomy, is admitted by the first authorities in comparative anatomy. The minute limbs hidden beneath the skin in many of the snake-like lizards, the anal hooks of the boa constrictor, the complete series of jointed finger-bones in the paddle of the Manatus and whale, are a few of the most familiar instances. In botany a similar class of facts has been long recognised. Abortive stamens, rudimentary floral envelopes and undeveloped carpels, are of the most frequent occurrence. To every thoughtful naturalist the question must arise, What are these for? What have they to do with the great laws of creation?

Do they not teach us something of the system of Nature? If each species has been created independently, and without any necessary relations with pre-existing species, what do these rudiments, these apparent imperfections mean? There must be a cause for them; they must be the necessary results of some great natural law. Now, if, as it has been endeavoured to be shown, the great law which has regulated the peopling of the earth with animal and vegetable life is, that every change shall be gradual; that no new creature shall be formed widely differing from anything before existing; that in this, as in everything else in Nature, there shall be gradation and harmony,—then these rudimentary organs are necessary, and are an essential part of the system of Nature. Ere the higher Vertebrata were formed, for instance, many steps were required, and many organs had to undergo modifications from the rudimental condition in which only they had as yet existed. We still see remaining an antitypal sketch of a wing adapted for flight in the scaly flapper of the penguin, and limbs first concealed beneath the skin, and then weakly protruding from it, were the necessary gradations before others should be formed fully adapted for locomotion.* Many more of these modifications should we behold, and more complete series

* The theory of Natural Selection has now taught us that these are not the steps by which limbs have been formed; and that most rudimentary organs have been produced by abortion, owing to disease, as explained by Mr. Darwin.

of them, had we a view of all the forms which have ceased to live. The great gaps that exist between fishes, reptiles, birds, and mammals would then, no doubt, be softened down by intermediate groups, and the whole organic world would be seen to be an unbroken and harmonious system

Conclusion.

It has now been shown, though most briefly and imperfectly, how the law that "*Every species has come into existence coincident both in time and space with a pre-existing closely allied species,*" connects together and renders intelligible a vast number of independent and hitherto unexplained facts. The natural system of arrangement of organic beings, their geographical distribution, their geological sequence, the phænomena of representative and substituted groups in all their modifications, and the most singular peculiarities of anatomical structure, are all explained and illustrated by it, in perfect accordance with the vast mass of facts which the researches of modern naturalists have brought together, and, it is believed, not materially opposed to any of them. It also claims a superiority over previous hypotheses, on the ground that it not merely explains, but necessitates what exists. Granted the law, and many of the most important facts in Nature could not have been otherwise, but are almost as necessary deductions from it, as are the elliptic orbits of the planets from the law of gravitation.

II.

ON THE TENDENCY OF VARIETIES TO
DEPART INDEFINITELY FROM THE
ORIGINAL TYPE.*

Instability of Varieties supposed to prove the permanent distinctness of Species.

ONE of the strongest arguments which have been adduced to prove the original and permanent distinctness of species is, that *varieties* produced in a state of domesticity are more or less unstable, and often have a tendency, if left to themselves, to return to the normal form of the parent species; and this instability is considered to be a distinctive peculiarity of all varieties, even of those occurring among wild animals in a state of nature, and to constitute a provision for preserving unchanged the originally created distinct species.

In the absence or scarcity of facts and observations as to *varieties* occurring among wild animals, this argument has had great weight with naturalists, and has led to a very general and somewhat

* Written at Ternate, February, 1858; and published in the Journal of the Proceedings of the Linnæan Society for August, 1858.

prejudiced belief in the stability of species. Equally general, however, is the belief in what are called "permanent or true varieties,"—races of animals which continually propagate their like, but which differ so slightly (although constantly) from some other race, that the one is considered to be a *variety* of the other. Which is the *variety* and which the original *species*, there is generally no means of determining, except in those rare cases in which the one race has been known to produce an offspring unlike itself and resembling the other. This, however, would seem quite incompatible with the "permanent invariability of species," but the difficulty is overcome by assuming that such varieties have strict limits, and can never again vary further from the original type, although they may return to it, which, from the analogy of the domesticated animals, is considered to be highly probable, if not certainly proved.

It will be observed that this argument rests entirely on the assumption, that *varieties* occurring in a state of nature are in all respects analogous to or even identical with those of domestic animals, and are governed by the same laws as regards their permanence or further variation. But it is the object of the present paper to show that this assumption is altogether false, that there is a general principle in nature which will cause many *varieties* to survive the parent species, and to give rise to successive variations departing further and further from the

original type, and which also produces, in domesticated animals, the tendency of varieties to return to the parent form.

The Struggle for Existence.

The life of wild animals is a struggle for existence. The full exertion of all their faculties and all their energies is required to preserve their own existence and provide for that of their infant offspring. The possibility of procuring food during the least favourable seasons, and of escaping the attacks of their most dangerous enemies, are the primary conditions which determine the existence both of individuals and of entire species. These conditions will also determine the population of a species; and by a careful consideration of all the circumstances we may be enabled to comprehend, and in some degree to explain, what at first sight appears so inexplicable—the excessive abundance of some species, while others closely allied to them are very rare.

The Law of Population of Species.

The general proportion that must obtain between certain groups of animals is readily seen. Large animals cannot be so abundant as small ones; the carnivora must be less numerous than the herbivora; eagles and lions can never be so plentiful as pigeons and antelopes; and the wild asses of the Tartarian deserts cannot equal in numbers the horses of the more luxuriant prairies and pampas of America. The

greater or less fecundity of an animal is often considered to be one of the chief causes of its abundance or scarcity; but a consideration of the facts will show us that it really has little or nothing to do with the matter. Even the least prolific of animals would increase rapidly if unchecked, whereas it is evident that the animal population of the globe must be stationary, or perhaps, through the influence of man, decreasing. Fluctuations there may be; but permanent increase, except in restricted localities, is almost impossible. For example, our own observation must convince us that birds do not go on increasing every year in a geometrical ratio, as they would do, were there not some powerful check to their natural increase. Very few birds produce less than two young ones each year, while many have six, eight, or ten; four will certainly be below the average; and if we suppose that each pair produce young only four times in their life, that will also be below the average, supposing them not to die either by violence or want of food. Yet at this rate how tremendous would be the increase in a few years from a single pair! A simple calculation will show that in fifteen years each pair of birds would have increased to nearly ten millions!* whereas we have no reason to believe that the number of the birds of any country increases at all in fifteen or in one hundred and fifty years. With such powers of in-

* This is under estimated. The number would really amount to more than two thousand millions!

crease the population must have reached its limits, and have become stationary, in a very few years after the origin of each species. It is evident, therefore, that each year an immense number of birds must perish—as many in fact as are born; and as on the lowest calculation the progeny are each year twice as numerous as their parents, it follows that, whatever be the average number of individuals existing in any given country, *twice that number must perish annually*,—a striking result, but one which seems at least highly probable, and is perhaps under rather than over the truth. It would therefore appear that, as far as the continuance of the species and the keeping up the average number of individuals are concerned, large broods are superfluous. On the average all above *one* become food for hawks and kites, wild cats or weasels, or perish of cold and hunger as winter comes on. This is strikingly proved by the case of particular species; for we find that their abundance in individuals bears no relation whatever to their fertility in producing offspring.

Perhaps the most remarkable instance of an immense bird population is that of the passenger pigeon of the United States, which lays only one, or at most two eggs, and is said to rear generally but one young one. Why is this bird so extraordinarily abundant, while others producing two or three times as many young are much less plentiful? The explanation is not difficult. The food

most congenial to this species, and on which it thrives best, is abundantly distributed over a very extensive region, offering such differences of soil and climate, that in one part or another of the area the supply never fails. The bird is capable of a very rapid and long-continued flight, so that it can pass without fatigue over the whole of the district it inhabits, and as soon as the supply of food begins to fail in one place is able to discover a fresh feeding-ground. This example strikingly shows us that the procuring a constant supply of wholesome food is almost the sole condition requisite for ensuring the rapid increase of a given species, since neither the limited fecundity, nor the unrestrained attacks of birds of prey and of man are here sufficient to check it. In no other birds are these peculiar circumstances so strikingly combined. Either their food is more liable to failure, or they have not sufficient power of wing to search for it over an extensive area, or during some season of the year it becomes very scarce, and less wholesome substitutes have to be found; and thus, though more fertile in offspring, they can never increase beyond the supply of food in the least favourable seasons.

Many birds can only exist by migrating, when their food becomes scarce, to regions possessing a milder, or at least a different climate, though, as these migrating birds are seldom excessively abundant, it is evident that the countries they visit are

still deficient in a constant and abundant supply of wholesome food. Those whose organization does not permit them to migrate when their food becomes periodically scarce, can never attain a large population. This is probably the reasons why woodpeckers are scarce with us, while in the tropics they are among the most abundant of solitary birds. Thus the house sparrow is more abundant than the redbreast, because its food is more constant and plentiful,—seeds of grasses being preserved during the winter, and our farm-yards and stubble-fields furnishing an almost inexhaustible supply. Why, as a general rule, are aquatic, and especially sea birds, very numerous in individuals? Not because they are more prolific than others, generally the contrary; but because their food never fails, the sea-shores and river-banks daily swarming with a fresh supply of small mollusca and crustacea. Exactly the same laws will apply to mammals. Wild cats are prolific and have few enemies; why then are they never as abundant as rabbits? The only intelligible answer is, that their supply of food is more precarious. It appears evident, therefore, that so long as a country remains physically unchanged, the numbers of its animal population cannot materially increase. If one species does so, some others requiring the same kind of food must diminish in proportion. The numbers that die annually must be immense; and as the individual existence of each animal depends upon itself, those that die must be

the weakest—the very young, the aged, and the diseased—while those that prolong their existence can only be the most perfect in health and vigour—those who are best able to obtain food regularly, and avoid their numerous enemies. It is, as we commenced by remarking, “a struggle for existence,” in which the weakest and least perfectly organized must always succumb.

The Abundance or Rarity of a Species dependent upon its more or less perfect Adaptation to the Conditions of Existence.

It seems evident that what takes place among the individuals of a species must also occur among the several allied species of a group,—viz., that those which are best adapted to obtain a regular supply of food, and to defend themselves against the attacks of their enemies and the vicissitudes of the seasons, must necessarily obtain and preserve a superiority in population; while those species which from some defect of power or organization are the least capable of counteracting the vicissitudes of food-supply, &c., must diminish in numbers, and, in extreme cases, become altogether extinct. Between these extremes the species will present various degrees of capacity for ensuring the means of preserving life; and it is thus we account for the abundance or rarity of species. Our ignorance will generally prevent us from accurately tracing the effects to their causes; but could we become perfectly acquainted with the

organization and habits of the various species of animals, and could we measure the capacity of each for performing the different acts necessary to its safety and existence under all the varying circumstances by which it is surrounded, we might be able even to calculate the proportionate abundance of individuals which is the necessary result.

If now we have succeeded in establishing these two points—1st, *that the animal population of a country is generally stationary, being kept down by a periodical deficiency of food, and other checks; and, 2nd, that the comparative abundance or scarcity of the individuals of the several species is entirely due to their organization and resulting habits, which, rendering it more difficult to procure a regular supply of food and to provide for their personal safety in some cases than in others, can only be balanced by a difference in the population which have to exist in a given area*—we shall be in a condition to proceed to the consideration of *varieties*, to which the preceding remarks have a direct and very important application.

Useful Variations will tend to Increase; useless or hurtful Variations to Diminish.

Most or perhaps all the variations from the typical form of a species must have some definite effect, however slight, on the habits or capacities of the individuals. Even a change of colour might, by rendering them more or less distinguishable, affect their safety; a greater or less development of hair

might modify their habits. More important changes, such as an increase in the power or dimensions of the limbs or any of the external organs, would more or less affect their mode of procuring food or the range of country which they could inhabit. It is also evident that most changes would affect, either favourably or adversely, the powers of prolonging existence. An antelope with shorter or weaker legs must necessarily suffer more from the attacks of the feline carnivora; the passenger pigeon with less powerful wings would sooner or later be affected in its powers of procuring a regular supply of food; and in both cases the result must necessarily be a diminution of the population of the modified species. If, on the other hand, any species should produce a variety having slightly increased powers of preserving existence, that variety must inevitably in time acquire a superiority in numbers. These results must follow as surely as old age, intemperance, or scarcity of food produce an increased mortality. In both cases there may be many individual exceptions; but on the average the rule will invariably be found to hold good. All varieties will therefore fall into two classes—those which under the same conditions would never reach the population of the parent species, and those which would in time obtain and keep a numerical superiority. Now, let some alteration of physical conditions occur in the district—a long period of drought, a destruction of vegetation by locusts, the

irruption of some new carnivorous animal seeking "pastures new"—any change in fact tending to render existence more difficult to the species in question, and tasking its utmost powers to avoid complete extermination; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized variety would suffer first, and, were the pressure severe, must soon become extinct. The same causes continuing in action, the parent species would next suffer, would gradually diminish in numbers, and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety.

Superior Varieties will ultimately Extirpate the original Species.

The *variety* would now have replaced the *species*, of which it would be a more perfectly developed and more highly organized form. It would be in all respects better adapted to secure its safety, and to prolong its individual existence and that of the race. Such a variety *could not* return to the original form; for that form is an inferior one, and could never compete with it for existence. Granted, therefore, a "tendency" to reproduce the original type of the species, still the variety must ever re-

main preponderant in numbers, and under adverse physical conditions *again alone survive*. But this new, improved, and populous race might itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant. Here, then, we have *progression and continued divergence* deduced from the general laws which regulate the existence of animals in a state of nature, and from the undisputed fact that varieties do frequently occur. It is not, however, contended that this result would be invariable; a change of physical conditions in the district might at times materially modify it, rendering the race which had been the most capable of supporting existence under the former conditions now the least so, and even causing the extinction of the newer and, for a time, superior race, while the old or parent species and its first inferior varieties continued to flourish. Variations in unimportant parts might also occur, having no perceptible effect on the life-preserving powers; and the varieties so furnished might run a course parallel with the parent species, either giving rise to further variations or returning to the former type. All we argue for is, that certain varieties have a tendency to maintain their existence longer than the original species, and this tendency must make itself felt; for though the doctrine of chances or averages can never be trusted to

on a limited scale, yet, if applied to high numbers, the results come nearer to what theory demands, and, as we approach to an infinity of examples, become strictly accurate. Now the scale on which nature works is so vast—the numbers of individuals and the periods of time with which she deals approach so near to infinity, than any cause, however slight, and however liable to be veiled and counteracted by accidental circumstances, must in the end produce its full legitimate results.

The Partial Reversion of Domesticated Varieties explained.

Let us now turn to domesticated animals, and inquire how varieties produced among them are affected by the principles here enunciated. The essential difference in the condition of wild and domestic animals is this,—that among the former, their well-being and very existence depend upon the full exercise and healthy condition of all their senses and physical powers, whereas, among the latter, these are only partially exercised, and in some cases are absolutely unused. A wild animal has to search, and often to labour, for every mouthful of food—to exercise sight, hearing, and smell in seeking it, and in avoiding dangers, in procuring shelter from the inclemency of the seasons, and in providing for the subsistence and safety of its offspring. There is no muscle of its body that is not called into daily and hourly activity; there is no sense or faculty that is

not strengthened by continual exercise. The domestic animal, on the other hand, has food provided for it, is sheltered, and often confined, to guard it against the vicissitudes of the seasons, is carefully secured from the attacks of its natural enemies, and seldom even rears its young without human assistance. Half of its senses and faculties become quite useless, and the other half are but occasionally called into feeble exercise, while even its muscular system is only irregularly brought into action.

Now when a variety of such an animal occurs, having increased power or capacity in any organ or sense, such increase is totally useless, is never called into action, and may even exist without the animal ever becoming aware of it. In the wild animal, on the contrary, all its faculties and powers being brought into full action for the necessities of existence, any increase becomes immediately available, is strengthened by exercise, and must even slightly modify the food, the habits, and the whole economy of the race. It creates as it were a new animal, one of superior powers, and which will necessarily increase in numbers and outlive those which are inferior to it.

Again, in the domesticated animal all variations have an equal chance of continuance; and those which would decidedly render a wild animal unable to compete with its fellows and continue its existence are no disadvantage whatever in a state of domesticity. Our quickly fattening pigs, short-legged sheep

pouter pigeons, and poodle dogs could never have come into existence in a state of nature, because the very first step towards such inferior forms would have led to the rapid extinction of the race; still less could they now exist in competition with their wild allies. The great speed but slight endurance of the race horse, the unwieldy strength of the ploughman's team, would both be useless in a state of nature. If turned wild on the pampas, such animals would probably soon become extinct, or under favourable circumstances might each gradually lose those extreme qualities which would never be called into action, and in a few generations revert to a common type, which must be that in which the various powers and faculties are so proportioned to each other as to be best adapted to procure food and secure safety,—that in which by the full exercise of every part of its organisation the animal can alone continue to live. Domestic varieties, when turned wild, *must* return to something near the type of the original wild stock, *or become altogether extinct*.*

We see, then, that no inferences as to the permanence of varieties in a state of nature can be deduced from the observations of those occurring among domestic animals. The two are so much opposed to each other in every circumstance of their

* That is, they will vary, and the variations which tend to adapt them to the wild state, and therefore approximate them to wild animals, will be preserved. Those individuals which do not vary sufficiently will perish.

existence, that what applies to the one is almost sure not to apply to the other. Domestic animals are abnormal, irregular, artificial ; they are subject to variations which never occur and never can occur in a state of nature : their very existence depends altogether on human care ; so far are many of them removed from that just proportion of faculties, that true balance of organisation, by means of which alone an animal left to its own resources can preserve its existence and continue its race.

Lamarck's Hypothesis very different from that now advanced.

The hypothesis of Lamarck—that progressive changes in species have been produced by the attempts of animals to increase the development of their own organs, and thus modify their structure and habits—has been repeatedly and easily refuted by all writers on the subject of varieties and species, and it seems to have been considered that when this was done the whole question has been finally settled ; but the view here developed renders such hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature. The powerful retractile talons of the falcon- and the cat-tribes have not been produced or increased by the volition of those animals ; but among the different varieties which occurred in the earlier and less highly organized forms of these groups, *those always survived longest which had the*

greatest facilities for seizing their prey. Neither did the giraffe acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching it neck for the purpose, but because any varieties which occurred among its antitypes with a longer neck than usual *at once secured a fresh range of pasture over the same ground as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them.* Even the peculiar colours of many animals, more especially of insects, so closely resembling the soil or leaves or bark on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints may have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest.* We have also here an acting cause to account for that balance so often observed in nature,—a deficiency in one set of organs always being compensated by an increased development of some others—powerful wings accompanying weak feet, or great velocity making up for the absence of defensive weapons; for it has been shown that all varieties in which an unbalanced deficiency occurred could not long continue their existence. The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude,

because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow. An origin such as is here advocated will also agree with the peculiar character of the modifications of form and structure which obtain in organized beings—the many lines of divergence from a central type, the increasing efficiency and power of a particular organ through a succession of allied species, and the remarkable persistence of unimportant parts, such as colour, texture of plumage and hair, form of horns or crests, through a series of species differing considerably in more essential characters. It also furnishes us with a reason for that “more specialized structure” which Professor Owen states to be a characteristic of recent compared with extinct forms, and which would evidently be the result of the progressive modification of any organ applied to a special purpose in the animal economy.

Conclusion.

We believe we have now shown that there is a tendency in nature to the continued progression of certain classes of *varieties* further and further from the original type—a progression to which there appears no reason to assign any definite limits—and that the same principle which produces this result in a state of nature will also explain why domestic varieties have a tendency, when they become wild, to revert to the original type. This progression,

by minute steps, in various directions, but always checked and balanced by the necessary conditions, subject to which alone existence can be preserved, may, it is believed, be followed out so as to agree with all the phænomena presented by organized beings, their extinction and succession in past ages, and all the extraordinary modifications of form, instinct and habits which they exhibit.

III.

MIMICRY, AND OTHER PROTECTIVE RESEMBLANCES AMONG ANIMALS.

THERE is no more convincing proof of the truth of a comprehensive theory, than its power of absorbing and finding a place for new facts, and its capability of interpreting phænomena which had been previously looked upon as unaccountable anomalies. It is thus that the law of universal gravitation and the undulatory theory of light have become established and universally accepted by men of science. Fact after fact has been brought forward as being apparently inconsistent with them, and one after another these very facts have been shown to be the consequences of the laws they were at first supposed to disprove. A false theory will never stand this test. Advancing knowledge brings to light whole groups of facts which it cannot deal with, and its advocates steadily decrease in numbers, notwithstanding the ability and scientific skill with which it may have been supported. The great name of Edward Forbes did not prevent his theory of "Polarity in the distribution of Organic beings in Time" from dying a natural death; but the most striking illustration of the behaviour of a false theory is to be found in the "Circular and Quinarian System" of classification

propounded by MacLeay, and developed by Swainson, with an amount of knowledge and ingenuity that have rarely been surpassed. This theory was eminently attractive, both from its symmetry and completeness, and from the interesting nature of the varied analogies and affinities which it brought to light and made use of. The series of Natural History volumes in "Lardner's Cabinet Cyclopædia," in which Mr. Swainson developed it in most departments of the animal kingdom, made it widely known; and in fact for a long time these were the best and almost the only popular text-books for the rising generation of naturalists. It was favourably received too by the older school, which was perhaps rather an indication of its unsoundness. A considerable number of well-known naturalists either spoke approvingly of it, or advocated similar principles, and for a good many years it was decidedly in the ascendent. With such a favourable introduction, and with such talented exponents, it must have become established if it had had any germ of truth in it; yet it quite died out in a few short years, its very existence is now a matter of history; and so rapid was its fall that its talented creator, Swainson, perhaps lived to be the last man who believed in it.

Such is the course of a false theory. That of a true one is very different, as may be well seen by the progress of opinion on the subject of Natural Selection. In less than eight years "The Origin of Species" has produced conviction in the minds of

a majority of the most eminent living men of science. New facts, new problems, new difficulties as they arise are accepted, solved or removed by this theory; and its principles are illustrated by the progress and conclusions of every well established branch of human knowledge. It is the object of the present essay to show how it has recently been applied to connect together and explain a variety of curious facts which had long been considered as inexplicable anomalies.

Importance of the Principle of Utility.

Perhaps no principle has ever been announced so fertile in results as that which Mr. Darwin so earnestly impresses upon us, and which is indeed a necessary deduction from the theory of Natural Selection, namely—that none of the definite facts of organic nature, no special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species—can exist, but which must now be or once have been *useful* to the individuals or the races which possess them. This great principle gives us a clue which we can follow out in the study of many recondite phænomena, and leads us to seek a meaning and a purpose of some definite character in minutiae which we should be otherwise almost sure to pass over as insignificant or unimportant.

Popular Theories of Colour in Animals.

The adaptation of the external colouring of animals

to their conditions of life has long been recognised, and has been imputed either to an originally created specific peculiarity, or to the direct action of climate, soil, or food. Where the former explanation has been accepted, it has completely checked inquiry, since we could never get any further than the fact of the adaptation. There was nothing more to be known about the matter. The second explanation was soon found to be quite inadequate to deal with all the varied phases of the phænomena, and to be contradicted by many well-known facts. For example, wild rabbits are always of grey or brown tints well suited for concealment among grass and fern. But when these rabbits are domesticated, without any change of climate or food, they vary into white or black, and these varieties may be multiplied to any extent, forming white or black races. Exactly the same thing has occurred with pigeons; and in the case of rats and mice, the white variety has not been shown to be at all dependent on alteration of climate, food, or other external conditions. In many cases the wings of an insect not only assume the exact tint of the bark or leaf it is accustomed to rest on, but the form and veining of the leaf or the exact rugosity of the bark is imitated; and these detailed modifications cannot be reasonably imputed to climate or to food, since in many cases the species does not feed on the substance it resembles, and when it does, no reasonable connexion can be shown to exist between the supposed cause and the effect produced. It was

reserved for the theory of Natural Selection to solve all these problems, and many others which were not at first supposed to be directly connected with them. To make these latter intelligible, it will be necessary to give a sketch of the whole series of phænomena which may be classed under the head of useful or protective resemblances.

Importance of Concealment as Influencing Colour.

Concealment, more or less complete, is useful to many animals, and absolutely essential to some. Those which have numerous enemies from which they cannot escape by rapidity of motion, find safety in concealment. Those which prey upon others must also be so constituted as not to alarm them by their presence or their approach, or they would soon die of hunger. Now it is remarkable in how many cases nature gives this boon to the animal, by colouring it with such tints as may best serve to enable it to escape from its enemies or to entrap its prey. Desert animals as a rule are desert-coloured. The lion is a typical example of this, and must be almost invisible when crouched upon the sand or among desert rocks and stones. Antelopes are all more or less sandy-coloured. The camel is pre-eminently so. The Egyptian cat and the Pampas cat are sandy or carth-coloured. The Australian kangaroos are of the same tints, and the original colour of the wild horse is supposed to have been a sandy or clay-colour.

The desert birds are still more remarkably protected by their assimilative hues. The stonechats, the larks, the quails, the goatsuckers and the grouse, which abound in the North African and Asiatic deserts, are all tinted and mottled so as to resemble with wonderful accuracy the average colour and aspect of the soil in the district they inhabit. The Rev. H. Tristram, in his account of the ornithology of North Africa in the 1st volume of the "Ibis," says: "In the desert, where neither trees, brushwood, nor even undulation of the surface afford the slightest protection to its foes, a modification of colour which shall be assimilated to that of the surrounding country, is absolutely necessary. Hence *without exception* the upper plumage of *every bird*, whether lark, chat, sylvain, or sand-grouse, and also the fur of *all the smaller mammals*, and the skin of *all the snakes and lizards*, is of one uniform isabelline or sand colour." After the testimony of so able an observer it is unnecessary to adduce further examples of the protective colours of desert animals.

Almost equally striking are the cases of arctic animals possessing the white colour that best conceals them upon snowfields and icebergs. The polar bear is the only bear that is white, and it lives constantly among snow and ice. The arctic fox, the ermine and the alpine hare change to white in winter only, because in summer white would be more conspicuous than any other colour, and therefore a danger rather than a protection; but the

American polar hare, inhabiting regions of almost perpetual snow, is white all the year round. Other animals inhabiting the same Northern regions do not, however, change colour. The sable is a good example, for throughout the severity of a Siberian winter it retains its rich brown fur. But its habits are such that it does not need the protection of colour, for it is said to be able to subsist on fruits and berries in winter, and to be so active upon the trees as to catch small birds among the branches. So also the woodchuck of Canada has a dark-brown fur; but then it lives in burrows and frequents river banks, catching fish and small animals that live in or near the water.

Among birds, the ptarmigan is a fine example of protective colouring. Its summer plumage so exactly harmonizes with the lichen-coloured stones among which it delights to sit, that a person may walk through a flock of them without seeing a single bird; while in winter its white plumage is an almost equal protection. The snow-bunting, the jer-falcon, and the snowy owl are also white-coloured birds inhabiting the arctic regions, and there can be little doubt but that their colouring is to some extent protective.

Nocturnal animals supply us with equally good illustrations. Mice, rats, bats, and moles possess the least conspicuous of hues, and must be quite invisible at times when any light colour would be instantly seen. Owls and goatsuckers are of those dark mottled tints

that will assimilate with bark and lichen, and thus protect them during the day, and at the same time be inconspicuous in the dusk.

It is only in the tropics, among forests which never lose their foliage, that we find whole groups of birds whose chief colour is green. The parrots are the most striking example, but we have also a group of green pigeons in the East; and the barbets, leaf-thrushes, bee-eaters, white-eyes, turacos, and several smaller groups, have so much green in their plumage as to tend greatly to conceal them among the foliage.

Special Modifications of Colour.

The conformity of tint which has been so far shown to exist between animals and their habitations is of a somewhat general character; we will now consider the cases of more special adaptation. If the lion is enabled by his sandy colour readily to conceal himself by merely crouching down upon the desert, how, it may be asked, do the elegant markings of the tiger, the jaguar, and the other large cats agree with this theory? We reply that these are generally cases of more or less special adaptation. The tiger is a jungle animal, and hides himself among tufts of grass or of bamboos, and in these positions the vertical stripes with which his body is adorned must so assimilate with the vertical stems of the bamboo, as to assist greatly in concealing him from his approaching prey. How remarkable it is that besides the lion and tiger, almost all the other large cats

are arboreal in their habits, and almost all have ocellated or spotted skins, which must certainly tend to blend them with the background of foliage; while the one exception, the puma, has an ashy brown uniform fur, and has the habit of clinging so closely to a limb of a tree while waiting for his prey to pass beneath as to be hardly distinguishable from the bark.

Among birds, the ptarmigan, already mentioned, must be considered a remarkable case of special adaptation. Another is a South-American goatsucker (*Caprimulgus rupestris*) which rests in the bright sunshine on little bare rocky islets in the Upper Rio Negro, where its unusually light colours so closely resemble those of the rock and sand, that it can scarcely be detected till trodden upon.

The Duke of Argyll, in his "Reign of Law," has pointed out the admirable adaptation of the colours of the woodcock to its protection. The various browns and yellows and pale ash-colour that occur in fallen leaves are all reproduced in its plumage, so that when according to its habit it rests upon the ground under trees, it is almost impossible to detect it. In snipes the colours are modified so as to be equally in harmony with the prevalent forms and colours of marshy vegetation. Mr. J. M. Lester, in a paper read before the Rugby School Natural History Society, observes:—"The wood-dove, when perched amongst the branches of its favourite *fir*, is scarcely discernible; whereas, were it among some

lighter foliage, the blue and purple tints in its plumage would far sooner betray it. The robin redbreast too, although it might be thought that the red on its breast made it much easier to be seen, is in reality not at all endangered by it, since it generally contrives to get among some russet or yellow fading leaves, where the red matches very well with the autumn tints, and the brown of the rest of the body with the bare branches."

Reptiles offer us many similar examples. The most arboreal lizards, the iguanas, are as green as the leaves they feed upon, and the slender whip-snakes are rendered almost invisible as they glide among the foliage by a similar colouration. How difficult it is sometimes to catch sight of the little green tree-frogs sitting on the leaves of a small plant enclosed in a glass case in the Zoological Gardens; yet how much better concealed must they be among the fresh green damp foliage of a marshy forest. There is a North-American frog found on lichen-covered rocks and walls, which is so coloured as exactly to resemble them, and as long as it remains quiet would certainly escape detection. Some of the geckos which cling motionless on the trunks of trees in the tropics, are of such curiously marbled colours as to match exactly with the bark they rest upon.

In every part of the tropics there are tree-snakes that twist among boughs and shrubs, or lie coiled up on the dense masses of foliage. These are of many distinct groups, and comprise both venomous and

harmless genera; but almost all of them are of a beautiful green colour, sometimes more or less adorned with white or dusky bands and spots. There can be little doubt that this colour is doubly useful to them, since it will tend to conceal them from their enemies, and will lead their prey to approach them unconscious of danger. Dr. Gunther informs me that there is only one genus of true arboreal snakes (*Dipsas*) whose colours are rarely green, but are of various shades of black, brown, and olive, and these are all nocturnal reptiles, and there can be little doubt conceal themselves during the day in holes, so that the green protective tint would be useless to them, and they accordingly retain the more usual reptilian hues.

Fishes present similar instances. Many flat fish, as for example the flounder and the skate, are exactly the colour of the gravel or sand on which they habitually rest. Among the marine flower gardens of an Eastern coral reef the fishes present every variety of gorgeous colour, while the river fish even of the tropics rarely if ever have gay or conspicuous markings. A very curious case of this kind of adaptation occurs in the sea-horses (*Hippocampus*) of Australia, some of which bear long foliaceous appendages resembling seaweed, and are of a brilliant red colour; and they are known to live among seaweed of the same hue, so that when at rest they must be quite invisible. There are now in the aquarium of the Zoological Society some slender green pipe-fish which fasten themselves to any object at

the bottom by their prehensile tails, and float about with the current, looking exactly like some simple cylindrical algæ.

It is, however, in the insect world that this principle of the adaptation of animals to their environment is most fully and strikingly developed. In order to understand how general this is, it is necessary to enter somewhat into details, as we shall thereby be better able to appreciate the significance of the still more remarkable phenomena we shall presently have to discuss. It seems to be in proportion to their sluggish motions or the absence of other means of defence, that insects possess the protective colouring. In the tropics there are thousands of species of insects which rest during the day clinging to the bark of dead or fallen trees; and the greater portion of these are delicately mottled with gray and brown tints, which though symmetrically disposed and infinitely varied, yet blend so completely with the usual colours of the bark, that at two or three feet distance they are quite undistinguishable. In some cases a species is known to frequent only one species of tree. This is the case with the common South American long-horned beetle (*Onychocerus scorio*) which, Mr. Bates informed me, is found only on a rough-barked tree, called Tapiribá, on the Amazon. It is very abundant, but so exactly does it resemble the bark in colour and rugosity, and so closely does it cling to the branches, that until it moves it is absolutely invisible! An allied species (*O.*

concentricus) is found only at Pará, on a distinct species of tree, the bark of which it resembles with equal accuracy. Both these insects are abundant, and we may fairly conclude that the protection they derive from this strange concealment is at least one of the causes that enable the race to flourish.

Many of the species of *Cicindela*, or tiger beetle, will illustrate this mode of protection. Our common *Cicindela campestris* frequents grassy banks, and is of a beautiful green colour, while *C. maritima*, which is found only on sandy sea-shores, is of a pale bronzy yellow, so as to be almost invisible. A great number of the species found by myself in the Malay islands are similarly protected. The beautiful *Cicindela gloriosa*, of a very deep velvety green colour, was only taken upon wet mossy stones in the bed of a mountain stream, where it was with the greatest difficulty detected. A large brown species (*C. heros*) was found chiefly on dead leaves in forest paths; and one which was never seen except on the wet mud of salt marshes was of a glossy olive so exactly the colour of the mud as only to be distinguished when the sun shone, by its shadow! Where the sandy beach was coralline and nearly white, I found a very pale *Cicindela*; wherever it was volcanic and black, a dark species of the same genus was sure to be met with.

There are in the East small beetles of the family Buprestidæ which generally rest on the midrib of a leaf, and the naturalist often hesitates before picking them off, so closely do they resemble pieces of bird's

dung. Kirby and Spence mention the small beetle *Onthophilus sulcatus* as being like the seed of an umbelliferous plant; and another small weevil, which is much persecuted by predatory beetles of the genus *Harpalus*, is of the exact colour of loamy soil, and was found to be particularly abundant in loam pits. Mr. Bates mentions a small beetle (*Chlamys pilula*) which was undistinguishable by the eye from the dung of caterpillars, while some of the *Cassidæ*, from their hemispherical forms and pearly gold colour, resemble glittering dew-drops upon the leaves.

A number of our small brown and speckled weevils at the approach of any object roll off the leaf they are sitting on, at the same time drawing in their legs and antennæ, which fit so perfectly into cavities for their reception that the insect becomes a mere oval brownish lump, which it is hopeless to look for among the similarly coloured little stones and earth pellets among which it lies motionless.

The distribution of colour in butterflies and moths respectively is very instructive from this point of view. The former have all their brilliant colouring on the upper surface of all four wings, while the under surface is almost always soberly coloured, and often very dark and obscure. The moths on the contrary have generally their chief colour on the hind wings only, the upper wings being of dull, sombre, and often imitative tints, and these generally conceal the hind wings when the insects are in repose. This arrangement of the colours is therefore eminently protective,

because the butterfly always rests with his wings raised so as to conceal the dangerous brilliancy of his upper surface. It is probable that if we watched their habits sufficiently we should find the under surface of the wings of butterflies very frequently imitative and protective. Mr. T. W. Wood has pointed out that the little orange-tip butterfly often rests in the evening on the green and white flower heads of an umbelliferous plant, and that when observed in this position the beautiful green and white mottling of the under surface completely assimilates with the flower heads and renders the creature very difficult to be seen. It is probable that the rich dark colouring of the under side of our peacock, tortoiseshell, and red-admiral butterflies answers a similar purpose.

Two curious South American butterflies that always settle on the trunks of trees (*Gynecia dirce* and *Callizona aesta*) have the under surface curiously striped and mottled, and when viewed obliquely must closely assimilate with the appearance of the furrowed bark of many kinds of trees. But the most wonderful and undoubted case of protective resemblance in a butterfly which I have ever seen, is that of the common Indian *Kallima inachis*, and its Malayan ally, *Kallima paralekta*. The upper surface of these insects is very striking and showy, as they are of a large size, and are adorned with a broad band of rich orange on a deep bluish ground. The under side is very variable in colour, so that out of fifty specimens no two can be found exactly alike, but

every one of them will be of some shade of ash or brown or ochre, such as are found among dead, dry, or decaying leaves. The apex of the upper wings is produced into an acute point, a very common form in the leaves of tropical shrubs and trees, and the lower wings are also produced into a short narrow tail. Between these two points runs a dark curved line exactly representing the midrib of a leaf, and from this radiate on each side a few oblique lines, which serve to indicate the lateral veins of a leaf. These marks are more clearly seen on the outer portion of the base of the wings, and on the inner side towards the middle and apex, and it is very curious to observe how the usual marginal and transverse striæ of the group are here modified and strengthened so as to become adapted for an imitation of the venation of a leaf. We come now to a still more extraordinary part of the imitation, for we find representations of leaves in every stage of decay, variously blotched and mildewed and pierced with holes, and in many cases irregularly covered with powdery black dots gathered into patches and spots, so closely resembling the various kinds of minute fungi that grow on dead leaves that it is impossible to avoid thinking at first sight that the butterflies themselves have been attacked by real fungi.

But this resemblance, close as it is, would be of little use if the habits of the insect did not accord with it. If the butterfly sat upon leaves or upon flowers, or opened its wings so as to expose the upper surface, or

exposed and moved its head and antennæ as many other butterflies do, its disguise would be of little avail. We might be sure, however, from the analogy of many other cases, that the habits of the insect are such as still further to aid its deceptive garb; but we are not obliged to make any such supposition, since I myself had the good fortune to observe scores of *Kallima paralekta*, in Sumatra, and to capture many of them, and can vouch for the accuracy of the following details. These butterflies frequent dry forests and fly very swiftly. They were never seen to settle on a flower or a green leaf, but were many times lost sight of in a bush or tree of dead leaves. On such occasions they were generally searched for in vain, for while gazing intently at the very spot where one had disappeared, it would often suddenly dart out, and again vanish twenty or fifty yards further on. On one or two occasions the insect was detected reposing, and it could then be seen how completely it assimilates itself to the surrounding leaves. It sits on a nearly upright twig, the wings fitting closely back to back, concealing the antennæ and head, which are drawn up between their bases. The little tails of the hind wing touch the branch, and form a perfect stalk to the leaf, which is supported in its place by the claws of the middle pair of feet, which are slender and inconspicuous. The irregular outline of the wings gives exactly the perspective effect of a shrivelled leaf. We thus have size, colour, form, markings, and habits, all combining together to produce a disguise which may be

said to be absolutely perfect; and the protection which it affords is sufficiently indicated by the abundance of the individuals that possess it.

The Rev. Joseph Greene has called attention to the striking harmony between the colours of those British moths which are on the wing in autumn and winter, and the prevailing tints of nature at those seasons. In autumn various shades of yellow and brown prevail, and he shows that out of fifty-two species that fly at this season, no less than forty-two are of corresponding colours. *Orgyia antiqua*, *O. gonostigma*, the genera *Xanthia*, *Glæa*, and *Ennomos* are examples. In winter, gray and silvery tints prevail, and the genus *Chematobia* and several species of *Hybernia* which fly during this season are of corresponding hues. No doubt if the habits of moths in a state of nature were more closely observed, we should find many cases of special protective resemblance. A few such have already been noticed. *Agriopsis aprilina*, *Acronycta psi*, and many other moths which rest during the day on the north side of the trunks of trees can with difficulty be distinguished from the grey and green lichens that cover them. The lappet moth (*Gastropacha querci*) closely resembles both in shape and colour a brown dry leaf; and the well-known buff-tip moth, when at rest is like the broken end of a lichen-covered branch. There are some of the small moths which exactly resemble the dung of birds dropped on leaves, and on this point Mr. A. Sidgwick, in a paper read before the Rugby School Natural History Society, gives the

following original observation:—"I myself have more than once mistaken *Cilix compressa*, a little white and grey moth, for a piece of bird's dung dropped upon a leaf, and *vice versâ* the dung for the moth. *Bryophila Glandifera* and *Perla* are the very image of the mortar walls on which they rest; and only this summer, in Switzerland, I amused myself for some time in watching a moth, probably *Larentia tripunctaria*, fluttering about quite close to me, and then alighting on a wall of the stone of the district which it so exactly matched as to be quite invisible a couple of yards off." There are probably hosts of these resemblances which have not been observed, owing to the difficulty of finding many of the species in their stations of natural repose. Caterpillars are also similarly protected. Many exactly resemble in tint the leaves they feed upon; others are like little brown twigs, and many are so strangely marked or humped, that when motionless they can hardly be taken to be living creatures at all. Mr. Andrew Murray has remarked how closely the larva of the peacock moth (*Saturnia pavonia-minor*) harmonizes in its ground colour with that of the young buds of heather on which it feeds, and that the pink spots with which it is decorated correspond with the flowers and flower-buds of the same plant.

The whole order of Orthoptera, grasshoppers, locusts, crickets, &c., are protected by their colours harmonizing with that of the vegetation or the soil on which they live, and in no other group have we such striking examples of special resemblance. Most of the

tropical Mantidæ and Locustidæ are of the exact tint of the leaves on which they habitually repose, and many of them in addition have the veinings of their wings modified so as exactly to imitate that of a leaf. This is carried to the furthest possible extent in the wonderful genus, *Phyllium*, the "walking leaf," in which not only are the wings perfect imitations of leaves in every detail, but the thorax and legs are flat, dilated, and leaf-like; so that when the living insect is resting among the foliage on which it feeds, the closest observation is often unable to distinguish between the animal and the vegetable.

The whole family of the Phasmidæ, or spectres, to which this insect belongs, is more or less imitative, and a great number of the species are called "walking-stick insects," from their singular resemblance to twigs and branches. Some of these are a foot long and as thick as one's finger, and their whole colouring, form, rugosity, and the arrangement of the head, legs, and antennæ, are such as to render them absolutely identical in appearance with dead sticks. They hang loosely about shrubs in the forest, and have the extraordinary habit of stretching out their legs unsymmetrically, so as to render the deception more complete. One of these creatures obtained by myself in Borneo (*Ceroxylus laceratus*) was covered over with foliaceous excrescences of a clear olive green colour, so as exactly to resemble a stick grown over by a creeping moss or *jungermannia*. The Dyak who brought it me assured me it was grown over with moss although alive, and it was only after a

most minute examination that I could convince myself it was not so.

We need not adduce any more examples to show how important are the details of form and of colouring in animals, and that their very existence may often depend upon their being by these means concealed from their enemies. This kind of protection is found apparently in every class and order, for it has been noticed wherever we can obtain sufficient knowledge of the details of an animal's life-history. It varies in degree, from the mere absence of conspicuous colour or a general harmony with the prevailing tints of nature, up to such a minute and detailed resemblance to inorganic or vegetable structures as to realize the talisman of the fairy tale, and to give its possessor the power of rendering itself invisible.

Theory of Protective Colouring.

We will now endeavour to show how these wonderful resemblances have most probably been brought about. Returning to the higher animals, let us consider the remarkable fact of the rarity of white colouring in the mammalia or birds of the temperate or tropical zones in a state of nature. There is not a single white land-bird or quadruped in Europe, except the few arctic or alpine species, to which white is a protective colour. Yet in many of these creatures there seems to be no inherent tendency to avoid white, for directly they are domesticated white varieties arise, and appear to thrive as well as others. We have white mice and rats, white

cats, horses, dogs, and cattle, white poultry, pigeons, turkeys, and ducks, and white rabbits. Some of these animals have been domesticated for a long period, others only for a few centuries; but in almost every case in which an animal has been thoroughly domesticated, parti-coloured and white varieties are produced and become permanent.

It is also well known that animals in a state of nature produce white varieties occasionally. Blackbirds, starlings, and crows are occasionally seen white, as well as elephants, deer, tigers, hares, moles, and many other animals; but in no case is a permanent white race produced. Now there are no statistics to show that the normal-coloured parents produce white offspring oftener under domestication than in a state of nature, and we have no right to make such an assumption if the facts can be accounted for without it. But if the colours of animals do really, in the various instances already adduced, serve for their concealment and preservation, then white or any other conspicuous colour must be hurtful, and must in most cases shorten an animal's life. A white rabbit would be more surely the prey of hawk or buzzard, and the white mole, or field mouse, could not long escape from the vigilant owl. So, also, any deviation from those tints best adapted to conceal a carnivorous animal would render the pursuit of its prey much more difficult, would place it at a disadvantage among its fellows, and in a time of scarcity would probably cause it to starve to death. On the other hand, if an animal spreads from a

temperate into an arctic district, the conditions are changed. During a large portion of the year, and just when the struggle for existence is most severe, white is the prevailing tint of nature, and dark colours will be the most conspicuous. The white varieties will now have an advantage; they will escape from their enemies or will secure food, while their brown companions will be devoured or will starve; and as "like produces like" is the established rule in nature, the white race will become permanently established, and dark varieties, when they occasionally appear, will soon die out from their want of adaptation to their environment. In each case the fittest will survive, and a race will be eventually produced adapted to the conditions in which it lives.

We have here an illustration of the simple and effectual means by which animals are brought into harmony with the rest of nature. That slight amount of variability in every species, which we often look upon as something accidental or abnormal, or so insignificant as to be hardly worthy of notice, is yet the foundation of all those wonderful and harmonious resemblances which play such an important part in the economy of nature. Variation is generally very small in amount, but it is all that is required, because the change in the external conditions to which an animal is subject is generally very slow and intermittent. When these changes have taken place too rapidly, the result has often been the extinction of species; but the general rule is, that climatal and geological changes go on

slowly, and the slight but continual variations in the colour, form, and structure of all animals, has furnished individuals adapted to these changes, and who have become the progenitors of modified races. Rapid multiplication, incessant slight variation, and survival of the fittest—these are the laws which ever keep the organic world in harmony with the inorganic, and with itself. These are the laws which we believe have produced all the cases of protective resemblance already adduced, as well as those still more curious examples we have yet to bring before our readers.

It must always be borne in mind that the more wonderful examples, in which there is not only a general but a special resemblance—as in the walking leaf, the mossy phasma, and the leaf-winged butterfly—represent those few instances in which the process of modification has been going on during an immense series of generations. They all occur in the tropics, where the conditions of existence are the most favourable, and where climatic changes have for long periods been hardly perceptible. In most of them favourable variations both of colour, form, structure, and instinct or habit, must have occurred to produce the perfect adaptation we now behold. All these are known to vary, and favourable variations when not accompanied by others that were unfavourable, would certainly survive. At one time a little step might be made in this direction, at another time in that—a change of conditions might sometimes render useless that which it had taken ages to produce—great and sudden physi-

cal modifications might often produce the extinction of a race just as it was approaching perfection, and a hundred checks of which we can know nothing may have retarded the progress towards perfect adaptation; so that we can hardly wonder at there being so few cases in which a completely successful result has been attained as shown by the abundance and wide diffusion of the creatures so protected.

Objection that Colour, as being dangerous, should not exist in Nature.

It is as well here to reply to an objection that will no doubt occur to many readers—that if protection is so useful to all animals, and so easily brought about by variation and survival of the fittest, there ought to be no conspicuously-coloured creatures; and they will perhaps ask how we account for the brilliant birds, and painted snakes, and gorgeous insects, that occur abundantly all over the world. It will be advisable to answer this question rather fully, in order that we may be prepared to understand the phenomena of “mimicry,” which it is the special object of this paper to illustrate and explain.

The slightest observation of the life of animals will show us, that they escape from their enemies and obtain their food in an infinite number of ways; and that their varied habits and instincts are in every case adapted to the conditions of their existence. The porcupine and the hedgehog have a defensive armour that saves them from the attacks of most animals.

The tortoise is not injured by the conspicuous colours of his shell, because that shell is in most cases an effectual protection to him. The skunks of North America find safety in their power of emitting an unbearably offensive odour; the beaver in its aquatic habits and solidly constructed abode. In some cases the chief danger to an animal occurs at one particular period of its existence, and if that is guarded against its numbers can easily be maintained. This is the case with many birds, the eggs and young of which are especially obnoxious to danger, and we find accordingly a variety of curious contrivances to protect them. We have nests carefully concealed, hung from the slender extremities of grass or boughs over water, or placed in the hollow of a tree with a very small opening. When these precautions are successful, so many more individuals will be reared than can possibly find food during the least favourable seasons, that there will always be a number of weakly and inexperienced young birds who will fall a prey to the enemies of the race, and thus render necessary for the stronger and healthier individuals no other safeguard than their strength and activity. The instincts most favourable to the production and rearing of offspring will in these cases be most important, and the survival of the fittest will act so as to keep up and advance those instincts, while other causes which tend to modify colour and marking may continue their action almost unchecked.

It is perhaps in insects that we may best study the varied means by which animals are defended or con-

cealed. One of the uses of the phosphorescence with which many insects are furnished, is probably to frighten away their enemies; for Kirby and Spence state that a ground beetle (*Carabus*) has been observed running round and round a luminous centipede as if afraid to attack it. An immense number of insects have stings, and some stingless ants of the genus *Polyrachis* are armed with strong and sharp spines on the back, which must render them unpalatable to many of the smaller insectivorous birds. Many beetles of the family *Curculionidæ* have the wing cases and other external parts so excessively hard, that they cannot be pinned without first drilling a hole to receive the pin, and it is probable that all such find a protection in this excessive hardness. Great numbers of insects hide themselves among the petals of flowers, or in the cracks of bark and timber; and finally, extensive groups, and even whole orders have a more or less powerful and disgusting smell and taste, which they either possess permanently, or can emit at pleasure. The attitudes of some insects may also protect them, as the habit of turning up the tail by the harmless rove-beetles (*Staphylindidæ*) no doubt leads other animals besides children to the belief that they can sting. The curious attitude assumed by sphinx caterpillars is probably a safeguard, as well as the blood-red tentacles which can suddenly be thrown out from the neck, by the caterpillars of all the true swallow-tailed butterflies.

It is among the groups that possess some of these varied kinds of protection in a high degree, that we

find the greatest amount of conspicuous colour, or at least the most complete absence of protective imitation. The stinging Hymenoptera, wasps, bees, and hornets, are, as a rule, very showy and brilliant insects, and there is not a single instance recorded in which any one of them is coloured so as to resemble a vegetable or inanimate substance. The Chrysididæ, or golden wasps, which do not sting, possess as a substitute the power of rolling themselves up into a ball, which is almost as hard and polished as if really made of metal,—and they are all adorned with the most gorgeous colours. The whole order Hemiptera (comprising the bugs) emit a powerful odour, and they present a very large proportion of gay-coloured and conspicuous insects. The lady-birds (Coccinellidæ) and their allies the Eumorphidæ, are often brightly spotted, as if to attract attention; but they can both emit fluids of a very disagreeable nature, they are certainly rejected by some birds, and are probably never eaten by any.

The great family of ground beetles (Carabidæ) almost all possess a disagreeable and some a very pungent smell, and a few, called bombardier beetles, have the peculiar faculty of emitting a jet of very volatile liquid, which appears like a puff of smoke, and is accompanied by a distinct crepitating explosion. It is probably because these insects are mostly nocturnal and predacious that they do not present more vivid hues. They are chiefly remarkable for brilliant metallic tints or dull red patches when they are not wholly black, and are therefore very conspicuous by day, when insect-

eaters are kept off by their bad odour and taste, but are sufficiently invisible at night when it is of importance that their prey should not become aware of their proximity.

It seems probable that in some cases that which would appear at first to be a source of danger to its possessor may really be a means of protection. Many showy and weak-flying butterflies have a very broad expanse of wing, as in the brilliant blue *Morphos* of Brazilian forests, and the large Eastern *Papilios*; yet these groups are tolerably plentiful. Now, specimens of these butterflies are often captured with pierced and broken wings, as if they had been seized by birds from whom they had escaped; but if the wings had been much smaller in proportion to the body, it seems probable that the insect would be more frequently struck or pierced in a vital part, and thus the increased expanse of the wings may have been indirectly beneficial.

In other cases the capacity of increase in a species is so great that however many of the perfect insect may be destroyed, there is always ample means for the continuance of the race. Many of the flesh flies, gnats, ants, palm-tree weevils and locusts are in this category. The whole family of *Cetoniadæ* or rose chafers, so full of gaily-coloured species, are probably saved from attack by a combination of characters. They fly very rapidly with a zigzag or waving course; they hide themselves the moment they alight, either in the corolla of flowers, or in rotten wood, or in cracks and hollows of trees, and they are generally encased in a very hard

and polished coat of mail which may render them unsatisfactory food to such birds as would be able to capture them. The causes which lead to the development of colour have been here able to act unchecked, and we see the result in a large variety of the most gorgeously-coloured insects.

Here, then, with our very imperfect knowledge of the life-history of animals, we are able to see that there are widely varied modes by which they may obtain protection from their enemies or concealment from their prey. Some of these seem to be so complete and effectual as to answer all the wants of the race, and lead to the maintenance of the largest possible population. When this is the case, we can well understand that no further protection derived from a modification of colour can be of the slightest use, and the most brilliant hues may be developed without any prejudicial effect upon the species. On some of the laws that determine the development of colour something may be said presently. It is now merely necessary to show that concealment by obscure or imitative tints is only one out of very many ways by which animals maintain their existence; and having done this we are prepared to consider the phenomena of what has been termed "mimicry." It is to be particularly observed, however, that the word is not here used in the sense of voluntary imitation, but to imply a particular kind of resemblance—a resemblance not in internal structure but in external appearance—a resemblance in those parts only that catch the eye—a re-

semblance that deceives. As this kind of resemblance has the same effect as voluntary imitation or mimicry, and as we have no word that expresses the required meaning, "mimicry" was adopted by Mr. Bates (who was the first to explain the facts), and has led to some misunderstanding; but there need be none, if it is remembered that both "mimicry" and "imitation" are used in a metaphorical sense, as implying that close external likeness which causes things unlike in structure to be mistaken for each other.

Mimicry.

It has been long known to entomologists that certain insects bear a strange external resemblance to others belonging to distinct genera, families, or even orders, and with which they have no real affinity whatever. The fact, however, appears to have been generally considered as dependent upon some unknown law of "analogy"—some "system of nature," or "general plan," which had guided the Creator in designing the myriads of insect forms, and which we could never hope to understand. In only one case does it appear that the resemblance was thought to be useful, and to have been designed as a means to a definite and intelligible purpose. The flies of the genus *Volucella* enter the nests of bees to deposit their eggs, so that their larvæ may feed upon the larvæ of the bees, and these flies are each wonderfully like the bee on which it is parasitic. Kirby and Spence believed that this resemblance or "mimicry" was for the express purpose of

protecting the flies from the attacks of the bees, and the connection is so evident that it was hardly possible to avoid this conclusion. The resemblance, however, of moths to butterflies or to bees, of beetles to wasps, and of locusts to beetles, has been many times noticed by eminent writers; but scarcely ever till within the last few years does it appear to have been considered that these resemblances had any special purpose, or were of any direct benefit to the insects themselves. In this respect they were looked upon as accidental, as instances of the "curious analogies" in nature which must be wondered at but which could not be explained. Recently, however, these instances have been greatly multiplied; the nature of the resemblances has been more carefully studied, and it has been found that they are often carried out into such details as almost to imply a purpose of deceiving the observer. The phenomena, moreover, have been shown to follow certain definite laws, which again all indicate their dependence on the more general law of the "survival of the fittest," or "the preservation of favoured races in the struggle for life." It will, perhaps, be as well here to state what these laws or general conclusions are, and then to give some account of the facts which support them.

The first law is, that in an overwhelming majority of cases of mimicry, the animals (or the groups) which resemble each other inhabit the same country, the same district, and in most cases are to be found together on the very same spot.

The second law is, that these resemblances are not indiscriminate, but are limited to certain groups, which in every case are abundant in species and individuals, and can often be ascertained to have some special protection.

The third law is, that the species which resemble or "mimic" these dominant groups, are comparatively less abundant in individuals, and are often very rare.

These laws will be found to hold good, in all the cases of true mimicry among various classes of animals to which we have now to call the attention of our readers.

Mimicry among Lepidoptera.

As it is among butterflies that instances of mimicry are most numerous and most striking, an account of some of the more prominent examples in this group will first be given. There is in South America an extensive family of these insects, the Heliconidæ, which are in many respects very remarkable. They are so abundant and characteristic in all the woody portions of the American tropics, that in almost every locality they will be seen more frequently than any other butterflies. They are distinguished by very elongate wings, body, and antennæ, and are exceedingly beautiful and varied in their colours; spots and patches of yellow, red, or pure white upon a black, blue, or brown ground, being most general. They frequent the forests chiefly, and all fly slowly and weakly; yet although they are so conspicuous, and could certainly be caught by insectivorous

birds more easily than almost any other insects, their great abundance all over the wide region they inhabit shows that they are not so persecuted. It is to be especially remarked also, that they possess no adaptive colouring to protect them during repose, for the under side of their wings presents the same, or at least an equally conspicuous colouring as the upper side; and they may be observed after sunset suspended at the end of twigs and leaves where they have taken up their station for the night, fully exposed to the attacks of enemies if they have any. These beautiful insects possess, however, a strong pungent semi-aromatic or medicinal odour, which seems to pervade all the juices of their system. When the entomologist squeezes the breast of one of them between his fingers to kill it, a yellow liquid exudes which stains the skin, and the smell of which can only be got rid of by time and repeated washings. Here we have probably the cause of their immunity from attack, since there is a great deal of evidence to show that certain insects are so disgusting to birds that they will under no circumstances touch them. Mr. Stainton has observed that a brood of young turkeys greedily devoured all the worthless moths he had amassed in a night's "sugaring," yet one after another seized and rejected a single white moth which happened to be among them. Young pheasants and partridges which eat many kinds of caterpillars seem to have an absolute dread of that of the common currant moth, which they will never touch, and tomtits as well as other small birds appear never to eat

the same species. In the case of the Heliconidæ, however, we have some direct evidence to the same effect. In the Brazilian forests there are great numbers of insectivorous birds—as jacamars, trogons, and puffbirds—which catch insects on the wing, and that they destroy many butterflies is indicated by the fact that the wings of these insects are often found on the ground where their bodies have been devoured. But among these there are no wings of Heliconidæ, while those of the large showy Nymphalidæ, which have a much swifter flight, are often met with. Again, a gentleman who had recently returned from Brazil stated at a meeting of the Entomological Society that he once observed a pair of puffbirds catching butterflies, which they brought to their nest to feed their young; yet during half an hour they never brought one of the Heliconidæ, which were flying lazily about in great numbers, and which they could have captured more easily than any others. It was this circumstance that led Mr. Belt to observe them so long, as he could not understand why the most common insects should be altogether passed by. Mr. Bates also tells us that he never saw them molested by lizards or predacious flies, which often pounce on other butterflies.

If, therefore, we accept it as highly probable (if not proved) that the Heliconidæ are very greatly protected from attack by their peculiar odour and taste, we find it much more easy to understand their chief characteristics—their great abundance, their slow flight, their gaudy colours, and the entire absence of protective tints on

their under surfaces. This property places them somewhat in the position of those curious wingless birds of oceanic islands, the dodo, the apteryx, and the moas, which are with great reason supposed to have lost the power of flight on account of the absence of carnivorous quadrupeds. Our butterflies have been protected in a different way, but quite as effectually; and the result has been that as there has been nothing to escape from, there has been no weeding out of slow flyers, and as there has been nothing to hide from, there has been no extermination of the bright-coloured varieties, and no preservation of such as tended to assimilate with surrounding objects.

Now let us consider how this kind of protection must act. Tropical insectivorous birds very frequently sit on dead branches of a lofty tree, or on those which overhang forest paths, gazing intently around, and darting off at intervals to seize an insect at a considerable distance, which they generally return to their station to devour. If a bird began by capturing the slow-flying, conspicuous *Heliconidæ*, and found them always so disagreeable that it could not eat them, it would after a very few trials leave off catching them at all; and their whole appearance, form, colouring, and mode of flight is so peculiar, that there can be little doubt birds would soon learn to distinguish them at a long distance, and never waste any time in pursuit of them. Under these circumstances, it is evident that any other butterfly of a group which birds were accustomed to devour, would be almost equally well protected by closely resembling a *Heliconia*

externally, as if it acquired also the disagreeable odour; always supposing that there were only a few of them among a great number of the Heliconias. If the birds could not distinguish the two kinds externally, and there were on the average only one eatable among fifty uneatable, they would soon give up seeking for the eatable ones, even if they knew them to exist. If, on the other hand, any particular butterfly of an eatable group acquired the disagreeable taste of the Heliconias while it retained the characteristic form and colouring of its own group, this would be really of no use to it whatever; for the birds would go on catching it among its eatable allies (compared with which it would rarely occur), it would be wounded and disabled, even if rejected, and its increase would thus be as effectually checked as if it were devoured. It is important, therefore, to understand that if any one genus of an extensive family of eatable butterflies were in danger of extermination from insect-eating birds, and if two kinds of variation were going on among them, some individuals possessing a slightly disagreeable taste, others a slight resemblance to the Heliconidæ, this latter quality would be much more valuable than the former. The change in flavour would not at all prevent the variety from being captured as before, and it would almost certainly be thoroughly disabled before being rejected. The approach in colour and form to the Heliconidæ, however, would be at the very first a positive, though perhaps a slight advantage; for although at short distances this variety would be easily distinguished and devoured, yet

at a longer distance it might be mistaken for one of the uneatable group, and so be passed by and gain another day's life, which might in many cases be sufficient for it to lay a quantity of eggs and leave a numerous progeny, many of which would inherit the peculiarity which had been the safeguard of their parent.

Now, this hypothetical case is exactly realized in South America. Among the white butterflies forming the family Pieridæ (many of which do not greatly differ in appearance from our own cabbage butterflies) is a genus of rather small size (*Leptalis*), some species of which are white like their allies, while the larger number exactly resemble the *Heliconidæ* in the form and colouring of the wings. It must always be remembered that these two families are as absolutely distinguished from each other by structural characters as are the carnivora and the ruminants among quadrupeds, and that an entomologist can always distinguish the one from the other by the structure of the feet, just as certainly as a zoologist can tell a bear from a buffalo by the skull or by a tooth. Yet the resemblance of a species of the one family to another species in the other family was often so great, that both Mr. Bates and myself were many times deceived at the time of capture, and did not discover the distinctness of the two insects till a closer examination detected their essential differences. During his residence of eleven years in the Amazon valley, Mr. Bates found a number of species or varieties of *Leptalis*, each of which was a more or less exact copy of one of the *Heliconidæ* of the district

it inhabited; and the results of his observations are embodied in a paper published in the *Linnean Transactions*, in which he first explained the phenomena of "mimicry" as the result of natural selection, and showed its identity in cause and purpose with protective resemblance to vegetable or inorganic forms.

The imitation of the *Heliconidæ* by the *Leptalides* is carried out to a wonderful degree in form as well as in colouring. The wings have become elongated to the same extent, and the antennæ and abdomen have both become lengthened, to correspond with the unusual condition in which they exist in the former family. In colouration there are several types in the different genera of *Heliconidæ*. The genus *Mechanitis* is generally of a rich semi-transparent brown, banded with black and yellow; *Methona* is of large size, the wings transparent like horn, and with black transverse bands; while the delicate *Ithomias* are all more or less transparent, with black veins and borders, and often with marginal and transverse bands of orange red. These different forms are all copied by the various species of *Leptalis*, every band and spot and tint of colour, and the various degrees of transparency, being exactly reproduced. As if to derive all the benefit possible from this protective mimicry, the habits have become so modified that the *Leptalides* generally frequent the very same spots as their models, and have the same mode of flight; and as they are always very scarce (Mr. Bates estimating their numbers at about one to a thousand of the group they resemble), there is hardly a

possibility of their being found out by their enemies. It is also very remarkable that in almost every case the particular *Ithomias* and other species of *Heliconidæ* which they resemble, are noted as being very common species, swarming in individuals, and found over a wide range of country. This indicates antiquity and permanence in the species, and is exactly the condition most essential both to aid in the development of the resemblance, and to increase its utility.

But the *Leptalides* are not the only insects who have prolonged their existence by imitating the great protected group of *Heliconidæ*;—a genus of quite another family of most lovely small American butterflies, the *Erycinidæ*, and three genera of diurnal moths, also present species which often mimic the same dominant forms, so that some, as *Ithomia ileridina* of St. Paulo, for instance, have flying with them a few individuals of three widely different insects, which are yet disguised with exactly the same form, colour, and markings, so as to be quite undistinguishable when upon the wing. Again, the *Heliconidæ* are not the only group that are imitated, although they are the most frequent models. The black and red group of South American *Papilios*, and the handsome *Erycinian* genus *Stalachtis*, have also a few who copy them; but this fact offers no difficulty, since these two groups are almost as dominant as the *Heliconidæ*. They both fly very slowly, they are both conspicuously coloured, and they both abound in individuals; so that there is every reason to believe that they possess a protection of a similar kind

to the Heliconidæ, and that it is therefore equally an advantage to other insects to be mistaken for them. There is also another extraordinary fact that we are not yet in a position clearly to comprehend: some groups of the Heliconidæ themselves mimic other groups. Species of *Heliconia* mimic *Mechanitis*, and every species of *Napeogenes* mimics some other Heliconideous butterfly. This would seem to indicate that the distasteful secretion is not produced alike by all members of the family, and that where it is deficient protective imitation comes into play. It is this, perhaps, that has caused such a general resemblance among the Heliconidæ, such a uniformity of type with great diversity of colouring, since any aberration causing an insect to cease to look like one of the family would inevitably lead to its being attacked, wounded, and exterminated, even although it was not eatable.

In other parts of the world an exactly parallel series of facts have been observed. The Danaidæ and the Acræidæ of the Old World tropics form in fact one great group with the Heliconidæ. They have the same general form, structure, and habits: they possess the same protective odour, and are equally abundant in individuals, although not so varied in colour, blue and white spots on a black ground being the most general pattern. The insects which mimic these are chiefly *Papilios*, and *Diadema*, a genus allied to our peacock and tortoiseshell butterflies. In tropical Africa there is a peculiar group of the genus *Danais*, characterized by dark-brown and bluish-white colours, arranged in

bands or stripes. One of these, *Danais niavius*, is exactly imitated both by *Papilio hippocoon* and by *Diadema anhedon*; another, *Danais echeria*, by *Papilio cenea*; and in Natal a variety of the *Danais* is found having a white spot at the tip of wings, accompanied by a variety of the *Papilio* bearing a corresponding white spot. *Acræa gea* is copied in its very peculiar style of colouration by the female of *Papilio cynorta*, by *Panopæa hirce*, and by the female of *Elymnias phegea*. *Acræa euryta* of Calabar has a female variety of *Panopea hirce* from the same place which exactly copies it; and Mr. Trimen, in his paper on Mimetic Analogies among African Butterflies, published in the Transactions of the Linnæan Society for 1868, gives a list of no less than sixteen species and varieties of *Diadema* and its allies, and ten of *Papilio*, which in their colour and markings are perfect mimics of species or varieties of *Danais* or *Acræa* which inhabit the same districts.

Passing on to India, we have *Danais tytia*, a butterfly with semi-transparent bluish wings and a border of rich reddish brown. This remarkable style of colouring is exactly reproduced in *Papilio agestor* and in *Diadema nama*, and all three insects not unfrequently come together in collections made at Darjeeling. In the Philippine Islands the large and curious *Idea leuconœ* with its semi-transparent white wings, veined and spotted with black, is copied by the rare *Papilio idæoides* from the same islands.

In the Malay archipelago the very common and

beautiful *Euplæa midamus* is so exactly mimicked by two rare *Papilios* (*P. paradoxa* and *P. ænigma*) that I generally caught them under the impression that they were the more common species; and the equally common and even more beautiful *Euplæa rhadamanthus*, with its pure white bands and spots on a ground of glossy blue and black, is reproduced in the *Papilio caunus*. Here also there are species of *Diadema* imitating the same group in two or three instances; but we shall have to adduce these further on in connexion with another branch of the subject.

It has been already mentioned that in South America there is a group of *Papilios* which have all the characteristics of a protected race, and whose peculiar colours and markings are imitated by other butterflies not so protected. There is just such a group also in the East, having very similar colours and the same habits, and these also are mimicked by other species in the same genus not closely allied to them, and also by a few of other families. *Papilio hector*, a common Indian butterfly of a rich black colour spotted with crimson, is so closely copied by *Papilio romulus*, that the latter insect has been thought to be its female. A close examination shows, however, that it is essentially different, and belongs to another section of the genus. *Papilio antiphus* and *P. diphilus*, black swallow-tailed butterflies with cream-coloured spots, are so well imitated by varieties of *P. theseus*, that several writers have classed them as the same species. *Papilio liris*, found only in the island of Timor, is accompanied

there by *P. ænomaus*, the female of which so exactly resembles it that they can hardly be separated in the cabinet, and on the wing are quite undistinguishable. But one of the most curious cases is the fine yellow-spotted *Papilio cöon*, which is unmistakably imitated by the female tailed form of *Papilio memnon*. These are both from Sumatra; but in North India *P. cöon* is replaced by another species, which has been named *P. doubledayi*, having red spots instead of yellow; and in the same district the corresponding female tailed form of *Papilio androgeus*, sometimes considered a variety of *P. memnon*, is similarly red-spotted. Mr. Westwood has described some curious day-flying moths (*Epicopeia*) from North India, which have the form and colour of *Papilios* of this section, and two of these are very good imitations of *Papilio polydorus* and *Papilio varuna*, also from North India.

Almost all these cases of mimicry are from the tropics, where the forms of life are more abundant, and where insect development especially is of unchecked luxuriance; but there are also one or two instances in temperate regions. In North America, the large and handsome red and black butterfly *Danais erippus* is very common; and the same country is inhabited by *Limenitis archippus*, which closely resembles the *Danais*, while it differs entirely from every species of its own genus.

The only case of probable mimicry in our own country is the following:—A very common white moth (*Spilosoma menthastri*) was found by Mr. Stainton

to be rejected by young turkeys among hundreds of other moths on which they greedily fed. Each bird in succession took hold of this moth and threw it down again, as if too nasty to eat. Mr. Jenner Weir also found that this moth was refused by the Bullfinch, Chaffinch, Yellow Hammer, and Red Bunting, but eaten after much hesitation by the Robin. We may therefore fairly conclude that this species would be disagreeable to many other birds, and would thus have an immunity from attack, which may be the cause of its great abundance and of its conspicuous white colour. Now it is a curious thing that there is another moth, *Diaphora mendica*, which appears about the same time, and whose female only is white. It is about the same size as *Spilosoma menthastri*, and sufficiently resembles it in the dusk, and this moth is much less common. It seems very probable, therefore, that these species stand in the same relation to each other as the mimicking butterflies of various families do to the *Heliconidæ* and *Danaidæ*. It would be very interesting to experiment on all white moths, to ascertain if those which are most common are generally rejected by birds. It may be anticipated that they would be so, because white is the most conspicuous of all colours for nocturnal insects, and had they not some other protection would certainly be very injurious to them.

Lepidoptera mimicking other Insects.

In the preceding cases we have found *Lepidoptera* imitating other species of the same order, and such

species only as we have good reason to believe were free from the attacks of many insectivorous creatures ; but there are other instances in which they altogether lose the external appearance of the order to which they belong, and take on the dress of bees or wasps—insects which have an undeniable protection in their stings. The Sesiidæ and Ægeriidæ, two families of day-flying moths, are particularly remarkable in this respect, and a mere inspection of the names given to the various species shows how the resemblance has struck everyone. We have apiformis, vespiforme, ichneumoniforme, scoliæforme, sphegiforme (bee-like, wasp-like, ichneumon-like, &c.) and many others, all indicating a resemblance to stinging Hymenoptera. In Britain we may particularly notice *Sesia bombiliformis*, which very closely resembles the male of the large and common humble bee, *Bombus hortorum* ; *Sphecia craboniforme*, which is coloured like a hornet, and is (on the authority of Mr. Jenner Weir) much more like it when alive than when in the cabinet, from the way in which it carries its wings ; and the currant clear-wing, *Trochilium tipuliforme*, which resembles a small black wasp (*Odynerus sinuatus*) very abundant in gardens at the same season. It has been so much the practice to look upon these resemblances as mere curious analogies playing no part in the economy of nature, that we have scarcely any observations of the habits and appearance when alive of the hundreds of species of these groups in various parts of the world, or how far they are accompanied by Hymenoptera, which they specifically

resemble. There are many species in India (like those figured by Professor Westwood in his "Oriental Entomology") which have the hind legs very broad and densely hairy, so as exactly to imitate the brush-legged bees (*Scopulipedes*) which abound in the same country. In this case we have more than mere resemblance of colour, for that which is an important functional structure in the one group is imitated in another whose habits render it perfectly useless.

Mimicry among Beetles.

It may fairly be expected that if these imitations of one creature by another really serve as a protection to weak and decaying species, instances of the same kind will be found among other groups than the *Lepidoptera*; and such is the case, although they are seldom so prominent and so easily recognised as those already pointed out as occurring in that order. A few very interesting examples may, however, be pointed out in most of the other orders of insects. The *Coleoptera* or beetles that imitate other *Coleoptera* of distinct groups are very numerous in tropical countries, and they generally follow the laws already laid down as regulating these phenomena. The insects which others imitate always have a special protection, which leads them to be avoided as dangerous or uneatable by small insectivorous animals; some have a disgusting taste (analogous to that of the *Heliconidæ*); others have such a hard and stony covering that they cannot be crushed or digested; while a third set are very active,

and armed with powerful jaws, as well as having some disagreeable secretion. Some species of Eumorphidæ and Hispidæ, small flat or hemispherical beetles which are exceedingly abundant, and have a disagreeable secretion, are imitated by others of the very distinct group of Longicornes (of which our common musk-beetle may be taken as an example). The extraordinary little *Cyclopeplus batesii*, belongs to the same sub-family of this group as the *Onychocerus scorpio* and *O. concentricus*, which have already been adduced as imitating with such wonderful accuracy the bark of the trees they habitually frequent; but it differs totally in outward appearance from every one of its allies, having taken upon itself the exact shape and colouring of a globular *Corynomalus*, a little stinking beetle with clubbed antennæ. It is curious to see how these clubbed antennæ are imitated by an insect belonging to a group with long slender antennæ. The sub-family Anisocerinæ, to which *Cyclopeplus* belongs, is characterised by all its members possessing a little knob or dilatation about the middle of the antennæ. This knob is considerably enlarged in *C. batesii*, and the terminal portion of the antennæ beyond it is so small and slender as to be scarcely visible, and thus an excellent substitute is obtained for the short clubbed antennæ of the *Corynomalus*. *Erythroplatis corallifer* is another curious broad flat beetle, that no one would take for a Longicorn, since it almost exactly resembles *Cephalodonta spinipes*, one of the commonest of the South American Hispidæ; and what is still more

remarkable, another Longicorn of a distinct group, *Streptolabis hispoides*, was found by Mr. Bates, which resembles the same insect with equal minuteness,—a case exactly parallel to that among butterflies, where species of two or three distinct groups mimicked the same Heliconia. Many of the soft-winged beetles (Malacoderms) are excessively abundant in individuals, and it is probable that they have some similar protection, more especially as other species often strikingly resemble them. A Longicorn beetle, *Pæcilderma terminale*, found in Jamaica, is coloured exactly in the same way as a *Lycus* (one of the Malacoderms) from the same island. *Eroschema poweri*, a Longicorn from Australia, might certainly be taken for one of the same group, and several species from the Malay Islands are equally deceptive. In the Island of Celebes I found one of this group, having the whole body and elytra of a rich deep blue colour, with the head only orange; and in company with it an insect of a totally different family (Eucnemidæ) with identically the same colouration, and of so nearly the same size and form as to completely puzzle the collector on every fresh occasion of capturing them. I have been recently informed by Mr. Jenner Weir, who keeps a variety of small birds, that none of them will touch our common “soldiers and sailors” (species of Malacoderms), thus confirming my belief that they were a protected group, founded on the fact of their being at once very abundant, of conspicuous colours, and the objects of mimicry.

There are a number of the larger tropical weevils which have the elytra and the whole covering of the body so hard as to be a great annoyance to the entomologist, because in attempting to transfix them the points of his pins are constantly turned. I have found it necessary in these cases to drill a hole very carefully with the point of a sharp penknife before attempting to insert a pin. Many of the fine long-antennæd Anthribidæ (an allied group) have to be treated in the same way. We can easily understand that after small birds have in vain attempted to eat these insects, they should get to know them by sight, and ever after leave them alone, and it will then be an advantage for other insects which are comparatively soft and eatable, to be mistaken for them. We need not be surprised, therefore, to find that there are many Longicorns which strikingly resemble the "hard beetles" of their own district. In South Brazil, *Acanthotritus dorsalis* is strikingly like a *Curculio* of the hard genus *Heiliplus*, and Mr. Bates assures me that he found *Gymnocerus cratosomoides* (a Longicorn) on the same tree with a hard *Cratosomus* (a weevil), which it exactly mimics. Again, the pretty Longicorn, *Phacellocera batesii*, mimics one of the hard Anthribidæ of the genus *Ptychoderes*, having long slender antennæ. In the Moluccas we find *Cacia anthriboides*, a small Longicorn which might be easily mistaken for a very common species of Anthribidæ found in the same districts; and the very rare *Capnolymma stygium* closely imitates the common *Mecocerus gazella*, which abounded where it was taken. *Doliops curculionoides* and other allied

Longicorns from the Philippine Islands most curiously resemble, both in form and colouring, the brilliant Pachyrhynchi,—Curculionidæ, which are almost peculiar to that group of islands. The remaining family of Coleoptera most frequently imitated is the Cicindelidæ. The rare and curious Longicorn, *Collyrodes lacordairei*, has exactly the form and colouring of the genus *Collyris*, while an undescribed species of *Heteromera* is exactly like a *Therates*, and was taken running on the trunks of trees, as is the habit of that group. There is one curious example of a Longicorn mimicking a Longicorn, like the *Papilios* and *Heliconidæ* which mimic their own allies. *Agnia fasciata*, belonging to the sub-family *Hypselominæ*, and *Nemophas grayi*, belonging to the *Lamiinæ*, were taken in Amboyna on the same fallen tree at the same time, and were supposed to be the same species till they were more carefully examined, and found to be structurally quite different. The colouring of these insects is very remarkable, being rich steel-blue black, crossed by broad hairy bands of orange buff, and out of the many thousands of known species of Longicorns they are probably the only two which are so coloured. The *Nemophas grayi* is the larger, stronger, and better armed insect, and belongs to a more widely spread and dominant group, very rich in species and individuals, and is therefore most probably the subject of mimicry by the other species.

Beetles mimicking other Insects.

We will now adduce a few cases in which beetles

imitate other insects, and insects of other orders imitate beetles.

Charis melipona, a South American Longicorn of the family *Necydalidæ*, has been so named from its resemblance to a small bee of the genus *Melipona*. It is one of the most remarkable cases of mimicry, since the beetle has the thorax and body densely hairy like the bee, and the legs are tufted in a manner most unusual in the order *Coleoptera*. Another Longicorn, *Odontocera odyneroides*, has the abdomen banded with yellow, and constricted at the base, and is altogether so exactly like a small common wasp of the genus *Odynerus*, that Mr. Bates informs us he was afraid to take it out of his net with his fingers for fear of being stung. Had Mr. Bates's taste for insects been less omnivorous than it was, the beetle's disguise might have saved it from his pin, as it had no doubt often done from the beak of hungry birds. A larger insect, *Sphecomorpha chalybea*, is exactly like one of the large metallic blue wasps, and like them has the abdomen connected with the thorax by a pedicel, rendering the deception most complete and striking. Many Eastern species of Longicorns of the genus *Oberea*, when on the wing exactly resemble *Tenthredinidæ*, and many of the small species of *Hesthesis* run about on timber, and cannot be distinguished from ants. There is one genus of South American Longicorns that appears to mimic the shielded bugs of the genus *Scutellera*. The *Gymnocerous capucinus* is one of these, and is very like *Pachyotris fabricii*, one of the *Scutelleridæ*. The

beautiful *Gymnocerous dulcissimus* is also very like the same group of insects, though there is no known species that exactly corresponds to it; but this is not to be wondered at, as the tropical Hemiptera have been comparatively so little cared for by collectors.

Insects mimicking Species of other Orders.

The most remarkable case of an insect of another order mimicking a beetle is that of the *Condylodera tricondyloides*, one of the cricket family from the Philippine Islands, which is so exactly like a *Tricondyla* (one of the tiger beetles), that such an experienced entomologist as Professor Westwood placed it among them in his cabinet, and retained it there a long time before he discovered his mistake! Both insects run along the trunks of trees, and whereas *Tricondylas* are very plentiful, the insect that mimics it is, as in all other cases, very rare. Mr. Bates also informs us that he found at Santarem on the Amazon, a species of locust which mimicked one of the tiger beetles of the genus *Odontocheila*, and was found on the same trees which they frequented.

There are a considerable number of Diptera, or two-winged flies, that closely resemble wasps and bees, and no doubt derive much benefit from the wholesome dread which those insects excite. The *Midas* dives, and other species of large Brazilian flies, have dark wings and metallic blue elongate bodies, resembling the large stinging *Sphegidæ* of the same country; and a very large fly of the genus *Asilus* has

black-banded wings and the abdomen tipped with rich orange, so as exactly to resemble the fine bee *Euglossa dimidiata*, and both are found in the same parts of South America. We have also in our own country species of *Bombylius* which are almost exactly like bees. In these cases the end gained by the mimicry is no doubt freedom from attack, but it has sometimes an altogether different purpose. There are a number of parasitic flies whose larvæ feed upon the larvæ of bees, such as the British genus *Volucella* and many of the tropical *Bombylii*, and most of these are exactly like the particular species of bee they prey upon, so that they can enter their nests unsuspected to deposit their eggs. There are also bees that mimic bees. The cuckoo bees of the genus *Nomada* are parasitic on the *Andrenidæ*, and they resemble either wasps or species of *Andrena*; and the parasitic humble-bees of the genus *Apathus* almost exactly resemble the species of humble-bees in whose nests they are reared. Mr. Bates informs us that he found numbers of these "cuckoo" bees and flies on the Amazon, which all wore the livery of working bees peculiar to the same country.

There is a genus of small spiders in the tropics which feed on ants, and they are exactly like ants themselves, which no doubt gives them more opportunity of seizing their prey; and Mr. Bates found on the Amazon a species of *Mantis* which exactly resembled the white ants which it fed upon, as well as several species of crickets (*Scaphura*), which resembled in a wonderful manner different sand-wasps of large size, which are

constantly on the search for crickets with which to provision their nests.

Perhaps the most wonderful case of all is the large caterpillar mentioned by Mr. Bates, which startled him by its close resemblance to a small snake. The first three segments behind the head were dilatable at the will of the insect, and had on each side a large black pupillated spot, which resembled the eye of the reptile. Moreover, it resembled a poisonous viper, not a harmless species of snake, as was proved by the imitation of keeled scales on the crown produced by the recumbent feet, as the caterpillar threw itself backward!

The attitudes of many of the tropical spiders are most extraordinary and deceptive, but little attention has been paid to them. They often mimic other insects, and some, Mr. Bates assures us, are exactly like flower buds, and take their station in the axils of leaves, where they remain motionless waiting for their prey.

Cases of Mimicry among the Vertebrata.

Having thus shown how varied and extraordinary are the modes in which mimicry occurs among insects, we have now to enquire if anything of the same kind is to be observed among vertebrated animals. When we consider all the conditions necessary to produce a good deceptive imitation, we shall see at once that such can very rarely occur in the higher animals, since they possess none of those facilities for the almost infinite modifications of external form which exist in the very nature of insect organization. The outer covering of

insects being more or less solid and horny, they are capable of almost any amount of change of form and appearance without any essential modification internally. In many groups the wings give much of the character, and these organs may be much modified both in form and colour without interfering with their special functions. Again, the number of species of insects is so great, and there is such diversity of form and proportion in every group, that the chances of an accidental approximation in size, form, and colour, of one insect to another of a different group, are very considerable; and it is these chance approximations that furnish the basis of mimicry, to be continually advanced and perfected by the survival of those varieties only which tend in the right direction.

In the Vertebrata, on the contrary, the skeleton being internal the external form depends almost entirely on the proportions and arrangement of that skeleton, which again is strictly adapted to the functions necessary for the well-being of the animal. The form cannot therefore be rapidly modified by variation, and the thin and flexible integument will not admit of the development of such strange protuberances as occur continually in insects. The number of species of each group in the same country is also comparatively small, and thus the chances of that first accidental resemblance which is necessary for natural selection to work upon are much diminished. We can hardly see the possibility of a mimicry by which the elk could escape from the wolf, or the buffalo from the tiger.

There is, however, in one group of Vertebrata such a general similarity of form, that a very slight modification, if accompanied by identity of colour, would produce the necessary amount of resemblance; and at the same time there exist a number of species which it would be advantageous for others to resemble, since they are armed with the most fatal weapons of offence. We accordingly find that reptiles furnish us with a very remarkable and instructive case of true mimicry.

Mimicry among Snakes.

There are in tropical America a number of venomous snakes of the genus *Elaps*, which are ornamented with brilliant colours disposed in a peculiar manner. The ground colour is generally bright red, on which are black bands of various widths and sometimes divided into two or three by yellow rings. Now, in the same country are found several genera of harmless snakes, having no affinity whatever with the above, but coloured exactly the same. For example, the poisonous *Elaps fulvius* often occurs in Guatemala with simple black bands on a coral-red ground; and in the same country is found the harmless snake *Pliocerus equalis*, coloured and banded in identically the same manner. A variety of *Elaps corallinus* has the black bands narrowly bordered with yellow on the same red ground colour, and a harmless snake, *Homalocranium semicinctum*, has exactly the same markings, and both are found in Mexico. The deadly *Elaps lemniscatus* has the black bands very broad, and each of them divided

into three by narrow yellow rings; and this again is exactly copied by a harmless snake, *Pliocerus elapoides*, which is found along with its model in Mexico.

But, more remarkable still, there is in South America a third group of snakes, the genus *Oxyrhopus*, doubtfully venomous, and having no immediate affinity with either of the preceding, which has also the same curious distribution of colours, namely, variously disposed rings of red, yellow, and black; and there are some cases in which species of all three of these groups similarly marked inhabit the same district. For example, *Elaps mipartitus* has single black rings very close together. It inhabits the west side of the Andes, and in the same districts occur *Pliocerus euryzonus* and *Oxyrhopus petolaris*, which exactly copy its pattern. In Brazil *Elaps lemniscatus* is copied by *Oxyrhopus trigeminus*, both having black rings disposed in threes. In *Elaps hemiprichii* the ground colour appears to be black, with alternations of two narrow yellow bands and a broader red one; and of this pattern again we have an exact double in *Oxyrhopus formosus*, both being found in many localities of tropical South America.

What adds much to the extraordinary character of these resemblances is the fact, that nowhere in the world but in America are there any snakes at all which have this style of colouring. Dr. Gunther, of the British Museum, who has kindly furnished some of the details here referred to, assures me that this is the case; and that red, black, and yellow rings occur

together on no other snakes in the world but on Elaps and the species which so closely resemble it. In all these cases, the size and form as well as the colouration, are so much alike, that none but a naturalist would distinguish the harmless from the poisonous species.

Many of the small tree-frogs are no doubt also mimickers. When seen in their natural attitudes, I have been often unable to distinguish them from beetles or other insects sitting upon leaves, but regret to say I neglected to observe what species or groups they most resembled, and the subject does not yet seem to have attracted the attention of naturalists abroad.

Mimicry among Birds.

In the class of birds there are a number of cases that make some approach to mimicry, such as the resemblance of the cuckoos, a weak and defenceless group of birds, to hawks and Gallinacæ. There is, however, one example which goes much further than this, and seems to be of exactly the same nature as the many cases of insect mimicry which have been already given. In Australia and the Moluccas there is a genus of honeysuckers called *Tropidorhynchus*, good sized birds, very strong and active, having powerful grasping claws and long, curved, sharp beaks. They assemble together in groups and small flocks, and they have a very loud bawling note, which can be heard at a great distance, and serves to collect a number together in time of danger. They are very plentiful

and very pugnacious, frequently driving away crows, and even hawks, which perch on a tree where a few of them are assembled. They are all of rather dull and obscure colours. Now in the same countries there is a group of orioles, forming the genus *Mimeta*, much weaker birds, which have lost the gay colouring of their allies the golden orioles, being usually olive-green or brown; and in several cases these most curiously resemble the *Tropidorhynchus* of the same island. For example, in the island of Bouru is found the *Tropidorhynchus bouruensis*, of a dull earthy colour, and the *Mimeta bouruensis*, which resembles it in the following particulars:—The upper and under surfaces of the two birds are exactly of the same tints of dark and light brown; the *Tropidorhynchus* has a large bare black patch round the eyes; this is copied in the *Mimeta* by a patch of black feathers. The top of the head of the *Tropidorhynchus* has a scaly appearance from the narrow scale-formed feathers, which are imitated by the broader feathers of the *Mimeta* having a dusky line down each. The *Tropidorhynchus* has a pale ruff formed of curious recurved feathers on the nape (which has given the whole genus the name of Friar birds); this is represented in the *Mimeta* by a pale band in the same position. Lastly, the bill of the *Tropidorhynchus* is raised into a protuberant keel at the base, and the *Mimeta* has the same character, although it is not a common one in the genus. The result is, that on a superficial examination the birds are identical, although they have important structural differences,

and cannot be placed near each other in any natural arrangement. As a proof that the resemblance is really deceptive, it may be mentioned that the *Mimeta* is figured and described as a honeysucker in the costly "Voyage de l'Astrolabe," under the name of *Philedon bouruensis*!

Passing to the island of Ceram, we find allied species of both genera. The *Tropidorhynchus subcornutus* is of an earthy brown colour washed with yellow ochre, with bare orbits, dusky cheeks, and the usual pale recurved nape-ruff. The *Mimeta forsteni* is absolutely identical in the tints of every part of the body, the details of which are imitated in the same manner as in the Bouru birds already described. In two other islands there is an approximation towards mimicry, although it is not so perfect as in the two preceding cases. In Timor the *Tropidorhynchus timoriensis* is of the usual earthy brown above, with the nape-ruff very prominent, the cheeks black, the throat nearly white, and the whole under surface pale whitish brown. These various tints are all well reproduced in *Mimeta virescens*, the chief want of exact imitation being that the throat and breast of the *Tropidorhynchus* has a very scaly appearance, being covered with rigid pointed feathers which are not imitated in the *Mimeta*, although there are signs of faint dusky spots which may easily furnish the groundwork of a more exact imitation by the continued survival of favourable variations in the same direction. There is also a large knob at the base of the bill of the *Tropidorhynchus* which is not at all

imitated by the *Mimeta*. In the island of Morty (north of Gilolo) there exists the *Tropidorhynchus fuscicapillus*, of a dark sooty brown colour, especially on the head, while the under parts are rather lighter, and the characteristic ruff of the nape is wanting. Now it is curious that in the adjacent island of Gilolo should be found the *Mimeta phæochromus*, the upper surface of which is of exactly the same dark sooty tint as the *Tropidorhynchus*, and is the only known species that is of such a dark colour. The under side is not quite light enough, but it is a good approximation. This *Mimeta* is a rare bird, and may very probably exist in Morty, though not yet found there; or, on the other hand, recent changes in physical geography may have led to the restriction of the *Tropidorhynchus* to that island, where it is very common.

Here, then, we have two cases of perfect mimicry and two others of good approximation, occurring between species of the same two genera of birds; and in three of these cases the pairs that resemble each other are found together in the same island, and to which they are peculiar. In all these cases the *Tropidorhynchus* is rather larger than the *Mimeta*, but the difference is not beyond the limits of variation in species, and the two genera are somewhat alike in form and proportion. There are, no doubt, some special enemies by which many small birds are attacked, but which are afraid of the *Tropidorhynchus* (probably some of the hawks), and thus it becomes advantageous for the weak *Mimeta* to resemble the

strong, pugnacious, noisy, and very abundant *Tropidorhynchus*.

My friend, Mr. Osbert Salvin, has given me another interesting case of bird mimicry. In the neighbourhood of Rio Janeiro is found an insect-eating hawk (*Harpagus diodon*), and in the same district a bird-eating hawk (*Accipiter pileatus*) which closely resembles it. Both are of the same ashy tint beneath, with the thighs and under wing-coverts reddish brown, so that when on the wing and seen from below they are undistinguishable. The curious point, however, is that the *Accipiter* has a much wider range than the *Harpagus*, and in the regions where the insect-eating species is not found it no longer resembles it, the under wing-coverts varying to white; thus indicating that the red-brown colour is kept true by its being useful to the *Accipiter* to be mistaken for the insect-eating species, which birds have learnt not to be afraid of.

Mimicry among Mammals.

Among the Mammalia the only case which may be true mimicry is that of the insectivorous genus *Cladobates*, found in the Malay countries, several species of which very closely resemble squirrels. The size is about the same, the long bushy tail is carried in the same way, and the colours are very similar. In this case the use of the resemblance must be to enable the *Cladobates* to approach the insects or small birds on which it feeds, under the disguise of the harmless fruit-eating squirrel.

Objections to Mr. Bates' Theory of Mimicry.

Having now completed our survey of the most prominent and remarkable cases of mimicry that have yet been noticed, we must say something of the objections that have been made to the theory of their production given by Mr. Bates, and which we have endeavoured to illustrate and enforce in the preceding pages. Three counter explanations have been proposed. Professor Westwood admits the fact of the mimicry and its probable use to the insect, but maintains that each species was created a mimic for the purpose of the protection thus afforded it. Mr. Andrew Murray, in his paper on the "Disguises of Nature," inclines to the opinion that similar conditions of food and of surrounding circumstances have acted in some unknown way to produce the resemblances; and when the subject was discussed before the Entomological Society of London, a third objection was added—that heredity or the reversion to ancestral types of form and colouration, might have produced many of the cases of mimicry.

Against the special creation of mimicking species there are all the objections and difficulties in the way of special creation in other cases, with the addition of a few that are peculiar to it. The most obvious is, that we have gradations of mimicry and of protective resemblance—a fact which is strongly suggestive of a natural process having been at work. Another very serious objection is, that as mimicry has been shown to be useful only to those species and groups which

are rare and probably dying out, and would cease to have any effect should the proportionate abundance of the two species be reversed, it follows that on the special-creation theory the one species must have been created plentiful, the other rare; and, notwithstanding the many causes that continually tend to alter the proportions of species, these two species must have always been specially maintained at their respective proportions, or the very purpose for which they each received their peculiar characteristics would have completely failed. A third difficulty is, that although it is very easy to understand how mimicry may be brought about by variation and the survival of the fittest, it seems a very strange thing for a Creator to protect an animal by making it imitate another, when the very assumption of a Creator implies his power to create it so as to require no such circuitous protection. These appear to be fatal objections to the application of the special-creation theory to this particular case.

The other two supposed explanations, which may be shortly expressed as the theories of "similar conditions" and of "heredity," agree in making mimicry, where it exists, an adventitious circumstance not necessarily connected with the well-being of the mimicking species. But several of the most striking and most constant facts which have been adduced, directly contradict both these hypotheses. The law that mimicry is confined to a few groups only is one of these, for "similar conditions" must act more or less on all groups in a limited region, and "heredity" must

influence all groups related to each other in an equal degree. Again, the general fact that those species which mimic others are rare, while those which are imitated are abundant, is in no way explained by either of these theories, any more than is the frequent occurrence of some palpable mode of protection in the imitated species. "Reversion to an ancestral type" no way explains why the imitator and the imitated always inhabit the very same district, whereas allied forms of every degree of nearness and remoteness generally inhabit different countries, and often different quarters of the globe; and neither it, nor "similar conditions," will account for the likeness between species of distinct groups being superficial only—a disguise, not a true resemblance; for the imitation of bark, of leaves, of sticks, of dung; for the resemblance between species in different orders, and even different classes and sub-kingdoms; and finally, for the graduated series of the phenomena, beginning with a general harmony and adaptation of tint in autumn and winter moths and in arctic and desert animals, and ending with those complete cases of detailed mimicry which not only deceive predacious animals, but puzzle the most experienced insect collectors and the most learned entomologists.

Mimicry by Female Insects only.

But there is yet another series of phenomena connected with this subject, which considerably strengthens the view here adopted, while it seems quite incompa-

tible with either of the other hypotheses ; namely, the relation of protective colouring and mimicry to the sexual differences of animals. It will be clear to every one that if two animals, which as regards "external conditions" and "hereditary descent," are exactly alike, yet differ remarkably in colouration, one resembling a protected species and the other not, the resemblance that exists in one only can hardly be imputed to the influence of external conditions or as the effect of heredity. And if, further, it can be proved that the one requires protection more than the other, and that in several cases it is that one which mimics the protected species, while the one that least requires protection never does so, it will afford very strong corroborative evidence that there is a real connexion between the necessity for protection and the phenomenon of mimicry. Now the sexes of insects offer us a test of the nature here indicated, and appear to furnish one of the most conclusive arguments in favour of the theory that the phenomena termed "mimicry" are produced by natural selection.

The comparative importance of the sexes varies much in different classes of animals. In the higher vertebrates, where the number of young produced at a birth is small and the same individuals breed many years in succession, the preservation of both sexes is almost equally important. In all the numerous cases in which the male protects the female and her offspring, or helps to supply them with food, his importance in the economy of nature is proportionately increased,

though it is never perhaps quite equal to that of the female. In insects the case is very different; they pair but once in their lives, and the prolonged existence of the male is in most cases quite unnecessary for the continuance of the race. The female, however, must continue to exist long enough to deposit her eggs in a place adapted for the development and growth of the progeny. Hence there is a wide difference in the need for protection in the two sexes; and we should, therefore, expect to find that in some cases the special protection given to the female was in the male less in amount or altogether wanting. The facts entirely confirm this expectation. In the spectre insects (Phasmidæ) it is often the females alone that so strikingly resemble leaves, while the males show only a rude approximation. The male *Diadema misippus* is a very handsome and conspicuous butterfly, without a sign of protective or imitative colouring, while the female is entirely unlike her partner, and is one of the most wonderful cases of mimicry on record, resembling most accurately the common *Danais chrysippus*, in whose company it is often found. So in several species of South American *Pieris*, the males are white and black, of a similar type of colouring to our own "cabbage" butterflies, while the females are rich yellow and buff, spotted and marked so as exactly to resemble species of *Heliconidæ* with which they associate in the forest. In the Malay archipelago is found a *Diadema* which had always been considered a male insect on account of its glossy metallic-blue tints,

while its companion of sober brown was looked upon as the female. I discovered, however, that the reverse is the case, and that the rich and glossy colours of the female are imitative and protective, since they cause her exactly to resemble the common *Euploea midamus* of the same regions, a species which has been already mentioned in this essay as mimicked by another butterfly, *Papilio paradoxa*. I have since named this interesting species *Diadema anomala* (see the Transactions of the Entomological Society, 1869, p. 285). In this case, and in that of *Diadema misippus*, there is no difference in the habits of the two sexes, which fly in similar localities; so that the influence of "external conditions" cannot be invoked here as it has been in the case of the South American *Pieris pyrrha* and allies, where the white males frequent open sunny places, while the *Heliconia*-like females haunt the shades of the forest.

We may impute to the same general cause (the greater need of protection for the female, owing to her weaker flight, greater exposure to attack, and supreme importance)—the fact of the colours of female insects being so very generally duller and less conspicuous than those of the other sex. And that it is chiefly due to this cause rather than to what Mr. Darwin terms "sexual selection" appears to be shown by the otherwise inexplicable fact, that in the groups which have a protection of any kind independent of concealment, sexual differences of colour are either quite wanting or slightly developed. The

Heliconidæ and Danaidæ, protected by a disagreeable flavour, have the females as bright and conspicuous as the males, and very rarely differing at all from them. The stinging Hymenoptera have the two sexes equally well coloured. The Carabidæ, the Coccinellidæ, Chrysomelidæ, and the Telephori have both sexes equally conspicuous, and seldom differing in colours. The brilliant Curculios, which are protected by their hardness, are brilliant in both sexes. Lastly, the glittering Cetoniadæ and Buprestidæ, which seem to be protected by their hard and polished coats, their rapid motions, and peculiar habits, present few sexual differences of colour, while sexual selection has often manifested itself by structural differences, such as horns, spines, or other processes.

Cause of the dull Colours of Female Birds.

The same law manifests itself in Birds. The female while sitting on her eggs requires protection by concealment to a much greater extent than the male; and we accordingly find that in a large majority of the cases in which the male birds are distinguished by unusual brilliancy of plumage, the females are much more obscure, and often remarkably plain-coloured. The exceptions are such as eminently to prove the rule, for in most cases we can see a very good reason for them. In particular, there are a few instances among wading and gallinaceous birds in which the female has decidedly more brilliant colours than the male; but it is a most curious and interesting fact

that in most if not all these cases the males sit upon the eggs; so that this exception to the usual rule almost demonstrates that it is because the process of incubation is at once very important and very dangerous, that the protection of obscure colouring is developed. The most striking example is that of the gray phalarope (*Phalaropus fulicarius*). When in winter plumage, the sexes of this bird are alike in colouration, but in summer the female is much the most conspicuous, having a black head, dark wings, and reddish-brown back, while the male is nearly uniform brown, with dusky spots. Mr. Gould in his "Birds of Great Britain" figures the two sexes in both winter and summer plumage, and remarks on the strange peculiarity of the usual colours of the two sexes being reversed, and also on the still more curious fact that the "male alone sits on the eggs," which are deposited on the bare ground. In another British bird, the dotterell, the female is also larger and more brightly-coloured than the male; and it seems to be proved that the males assist in incubation even if they do not perform it entirely, for Mr. Gould tells us, "that they have been shot with the breast bare of feathers, caused by sitting on the eggs." The small quail-like birds forming the genus *Turnix* have also generally large and bright-coloured females, and we are told by Mr. Jerdon in his "Birds of India" that "the natives report that during the breeding season the females desert their eggs and associate in flocks while the males are employed in hatching the eggs."

It is also an ascertained fact, that the females are more bold and pugnacious than the males. A further confirmation of this view is to be found in the fact (not hitherto noticed) that in a large majority of the cases in which bright colours exist in both sexes incubation takes place in a dark hole or in a dome-shaped nest. Female kingfishers are often equally brilliant with the male, and they build in holes in banks. Bee-eaters, trogons, motmots, and toucans, all build in holes, and in none is there any difference in the sexes, although they are, without exception, showy birds. Parrots build in holes in trees, and in the majority of cases they present no marked sexual difference tending to concealment of the female. Woodpeckers are in the same category, since though the sexes often differ in colour, the female is not generally less conspicuous than the male. Wagtails and titmice build concealed nests, and the females are nearly as gay as their mates. The female of the pretty Australian bird *Pardalotus punctatus*, is very conspicuously spotted on the upper surface, and it builds in a hole in the ground. The gay-coloured hang-nests (*Icterinæ*) and the equally brilliant tanagers may be well contrasted; for the former, concealed in their covered nests, present little or no sexual difference of colour—while the open-nested tanagers have the females dull-coloured and sometimes with almost protective tints. No doubt there are many individual exceptions to the rule here indicated, because many and various causes have combined to determine both the colouration and the habits

of birds. These have no doubt acted and re-acted on each other; and when conditions have changed one of these characters may often have become modified, while the other, though useless, may continue by hereditary descent an apparent exception to what otherwise seems a very general rule. The facts presented by the sexual differences of colour in birds and their mode of nesting, are on the whole in perfect harmony with that law of protective adaptation of colour and form, which appears to have checked to some extent the powerful action of sexual selection, and to have materially influenced the colouring of female birds, as it has undoubtedly done that of female insects.

Use of the gaudy Colours of many Caterpillars.

Since this essay was first published a very curious difficulty has been cleared up by the application of the general principle of protective colouring. Great numbers of caterpillars are so brilliantly marked and coloured as to be very conspicuous even at a considerable distance, and it has been noticed that such caterpillars seldom hide themselves. Other species, however, are green or brown, closely resembling the colours of the substances on which they feed, while others again imitate sticks, and stretch themselves out motionless from a twig so as to look like one of its branches. Now, as caterpillars form so large a part of the food of birds, it was not easy to understand why any of them should have such bright colours and mark

ings as to make them specially visible. Mr. Darwin had put the case to me as a difficulty from another point of view, for he had arrived at the conclusion that brilliant colouration in the animal kingdom is mainly due to sexual selection, and this could not have acted in the case of sexless larvæ. Applying here the analogy of other insects, I reasoned, that since some caterpillars were evidently protected by their imitative colouring, and others by their spiny or hairy bodies, the bright colours of the rest must also be in some way useful to them. I further thought that as some butterflies and moths were greedily eaten by birds while others were distasteful to them, and these latter were mostly of conspicuous colours, so probably these brilliantly coloured caterpillars were distasteful, and therefore never eaten by birds. Distastefulness alone would however be of little service to caterpillars, because their soft and juicy bodies are so delicate, that if seized and afterwards rejected by a bird they would almost certainly be killed. Some constant and easily perceived signal was therefore necessary to serve as a warning to birds never to touch these uneatable kinds, and a very gaudy and conspicuous colouring with the habit of fully exposing themselves to view becomes such a signal, being in strong contrast with the green or brown tints and retiring habits of the eatable kinds. The subject was brought by me before the Entomological Society (see Proceedings, March 4th, 1867), in order that those members having opportunities for making observations might do so in the following summer; and I also wrote a letter to

the *Field* newspaper, begging that some of its readers would co-operate in making observations on what insects were rejected by birds, at the same time fully explaining the great interest and scientific importance of the problem. It is a curious example of how few of the country readers of that paper are at all interested in questions of simple natural history, that I only obtained one answer from a gentleman in Cumberland, who gave me some interesting observations on the general dislike and abhorrence of all birds to the "Gooseberry Caterpillar," probably that of the Magpie-moth (*Abraxas grossulariata*). Neither young pheasants, partridges, nor wild-ducks could be induced to eat it, sparrows and finches never touched it, and all birds to whom he offered it rejected it with evident dread and abhorrence. It will be seen that these observations are confirmed by those of two members of the Entomological Society to whom we are indebted for more detailed information.

In March, 1869, Mr. J. Jenner Weir communicated a valuable series of observations made during many years, but more especially in the two preceding summers, in his aviary, containing the following birds of more or less insectivorous habits:—Robin, Yellow-Hammer, Reed-bunting, Bullfinch, Chaffinch, Crossbill, Thrush, Tree-Pipit, Siskin, and Redpoll. He found that hairy caterpillars were uniformly rejected; five distinct species were quite unnoticed by all his birds, and were allowed to crawl about the aviary for days with impunity. The spiny caterpillars of the Tortoiseshell and Peacock but-

terflies were equally rejected; but in both these cases Mr. Weir thinks it is the taste, not the hairs or spines, that are disagreeable, because some very young caterpillars of a hairy species were rejected although no hairs were developed, and the smooth pupæ of the above-named butterflies were refused as persistently as the spined larvæ. In these cases, then, both hairs and spines would seem to be mere signs of uneatableness.

His next experiments were with those smooth gaily-coloured caterpillars which never conceal themselves, but on the contrary appear to court observation. Such are those of the Magpie moth (*Abraxas grossulariata*), whose caterpillar is conspicuously white and black spotted—the *Diloba cœruleocephala*, whose larvæ is pale yellow with a broad blue or green lateral band—the *Cucullia verbasci*, whose larvæ is greenish white with yellow bands and black spots, and *Anthrocera filipendulæ* (the six spot Burnet moth), whose caterpillar is yellow with black spots. These were given to the birds at various times, sometimes mixed with other kinds of larvæ which were greedily eaten, but they were in every case rejected apparently unnoticed, and were left to crawl about till they died.

The next set of observations were on the dull-coloured and protected larvæ, and the results of numerous experiments are thus summarised by Mr. Weir. “All caterpillars whose habits are nocturnal, which are dull coloured, with fleshy bodies and smooth skins, are eaten with the greatest avidity. Every species of green caterpillar is also much re-

lished. All Geometræ, whose larvæ resemble twigs as they stand out from the plant on their anal prolegs, are invariably eaten.”

At the same meeting Mr. A. G. Butler, of the British Museum, communicated the results of his observations with lizards, frogs, and spiders, which strikingly corroborate those of Mr. Weir. Three green lizards (*Lacerta viridis*) which he kept for several years, were very voracious, eating all kinds of food, from a lemon cheesecake to a spider, and devouring flies, caterpillars, and humble bees; yet there were some caterpillars and moths which they would seize only to drop immediately. Among these the principal were the caterpillar of the Magpie moth (*Abraxas grossulariata*) and the perfect six spot Burnet moth (*Anthrocera filipendulæ*). These would be first seized but invariably dropped in disgust, and afterwards left unmolested. Subsequently frogs were kept and fed with caterpillars from the garden, but two of these—that of the before-mentioned Magpie moth, and that of the V. moth (*Halia wavaria*), which is green with conspicuous white or yellow stripes and black spots—were constantly rejected. When these species were first offered, the frogs sprang at them eagerly and licked them into their mouths; no sooner, however, had they done so than they seemed to be aware of the mistake that they had made, and sat with gaping mouths, rolling their tongues about until they had got quit of the nauseous morsels.

With spiders the same thing occurred. These two

caterpillars were repeatedly put into the webs both of the geometrical and hunting spiders (*Epeira diadema* and *Lycosa* sp.), but in the former case they were cut out and allowed to drop; in the latter, after disappearing in the jaws of their captor down his dark silken funnel, they invariably reappeared, either from below or else taking long strides up the funnel again. Mr. Butler has observed lizards fight with and finally devour humble bees, and a frog sitting on a bed of stone-crop leap up and catch the bees which flew over his head, and swallow them, in utter disregard of their stings. It is evident, therefore, that the possession of a disagreeable taste or odour is a more effectual protection to certain conspicuous caterpillars and moths, than would be even the possession of a sting.

The observations of these two gentlemen supply a very remarkable confirmation of the hypothetical solution of the difficulty which I had given two years before. And as it is generally acknowledged that the best test of the truth and completeness of a theory is the power which it gives us of prevision, we may I think fairly claim this as a case in which the power of prevision has been successfully exerted, and therefore as furnishing a very powerful argument in favour of the truth of the theory of Natural Selection.

Summary.

I have now completed a brief, and necessarily very imperfect, survey of the various ways in which the

external form and colouring of animals is adapted to be useful to them, either by concealing them from their enemies or from the creatures they prey upon. It has, I hope, been shown that the subject is one of much interest, both as regard a true comprehension of the place each animal fills in the economy of nature, and the means by which it is enabled to maintain that place; and also as teaching us how important a part is played by the minutest details in the structure of animals, and how complicated and delicate is the equilibrium of the organic world.

My exposition of the subject having been necessarily somewhat lengthy and full of details, it will be as well to recapitulate its main points.

There is a general harmony in nature between the colours of an animal and those of its habitation. Arctic animals are white, desert animals are sand-coloured; dwellers among leaves and grass are green; nocturnal animals are dusky. These colours are not universal, but are very general, and are seldom reversed. Going on a little further, we find birds, reptiles, and insects, so tinted and mottled as exactly to match the rock, or bark, or leaf, or flower, they are accustomed to rest upon,—and thereby effectually concealed. Another step in advance, and we have insects which are formed as well as coloured so as exactly to resemble particular leaves, or sticks, or mossy twigs, or flowers; and in these cases very peculiar habits and instincts come into play to aid in the deception and render the concealment more

complete. We now enter upon a new phase of the phenomena, and come to creatures whose colours neither conceal them nor make them like vegetable or mineral substances; on the contrary, they are conspicuous enough, but they completely resemble some other creature of a quite different group, while they differ much in outward appearance from those with which all essential parts of their organization show them to be really closely allied. They appear like actors or masqueraders dressed up and painted for amusement, or like swindlers endeavouring to pass themselves off for well-known and respectable members of society. What is the meaning of this strange travestie? Does Nature descend to imposture or masquerade? We answer, she does not. Her principles are too severe. There is a use in every detail of her handiwork. The resemblance of one animal to another is of exactly the same essential nature as the resemblance to a leaf, or to bark, or to desert sand, and answers exactly the same purpose. In the one case the enemy will not attack the leaf or the bark, and so the disguise is a safeguard; in the other case it is found that for various reasons the creature resembled is passed over, and not attacked by the usual enemies of its order, and thus the creature that resembles it has an equally effectual safeguard. We are plainly shown that the disguise is of the same nature in the two cases, by the occurrence in the same group of one species resembling a vegetable substance, while another resembles a living animal of

another group; and we know that the creatures resembled, possess an immunity from attack, by their being always very abundant, by their being conspicuous and not concealing themselves, and by their having generally no visible means of escape from their enemies; while, at the same time, the particular quality that makes them disliked is often very clear, such as a nasty taste or an indigestible hardness. Further examination reveals the fact that, in several cases of both kinds of disguise, it is the female only that is thus disguised; and as it can be shown that the female needs protection much more than the male, and that her preservation for a much longer period is absolutely necessary for the continuance of the race, we have an additional indication that the resemblance is in all cases subservient to a great purpose—the preservation of the species.

In endeavouring to explain these phenomena as having been brought about by variation and natural selection, we start with the fact that white varieties frequently occur, and when protected from enemies show no incapacity for continued existence and increase. We know, further, that varieties of many other tints occasionally occur; and as “the survival of the fittest” must inevitably weed out those whose colours are prejudicial and preserve those whose colours are a safeguard, we require no other mode of accounting for the protective tints of arctic and desert animals. But this being granted, there is such a perfectly continuous and graduated series of

examples of every kind of protective imitation, up to the most wonderful cases of what is termed "mimicry," that we can find no place at which to draw the line, and say,—so far variation and natural selection will account for the phenomena, but for all the rest we require a more potent cause. The counter theories that have been proposed, that of the "special creation" of each imitative form, that of the action of "similar conditions of existence" for some of the cases, and of the laws of "hereditary descent and the reversion to ancestral forms" for others,—have all been shown to be beset with difficulties, and the two latter to be directly contradicted by some of the most constant and most remarkable of the facts to be accounted for.

General deductions as to Colour in Nature.

The important part that "protective resemblance" has played in determining the colours and markings of many groups of animals, will enable us to understand the meaning of one of the most striking facts in nature, the uniformity in the colours of the vegetable as compared with the wonderful diversity of the animal world. There appears no good reason why trees and shrubs should not have been adorned with as many varied hues and as strikingly designed patterns as birds and butterflies, since the gay colours of flowers show that there is no incapacity in vegetable tissues to exhibit them. But even flowers themselves present us with none of those wonderful designs, those complicated arrangements of stripes and dots

and patches of colour, that harmonious blending of hues in lines and bands and shaded spots, which are so general a feature in insects. It is the opinion of Mr. Darwin that we owe much of the beauty of flowers to the necessity of attracting insects to aid in their fertilisation, and that much of the development of colour in the animal world is due to "sexual selection," colour being universally attractive, and thus leading to its propagation and increase; but while fully admitting this, it will be evident from the facts and arguments here brought forward, that very much of the *variety* both of colour and markings among animals is due to the supreme importance of concealment, and thus the various tints of minerals and vegetables have been directly reproduced in the animal kingdom, and again and again modified as more special protection became necessary. We shall thus have two causes for the development of colour in the animal world, and shall be better enabled to understand how, by their combined and separate action, the immense variety we now behold has been produced. Both causes, however, will come under the general law of "Utility," the advocacy of which, in its broadest sense, we owe almost entirely to Mr. Darwin. A more accurate knowledge of the varied phenomena connected with this subject may not improbably give us some information both as to the senses and the mental faculties of the lower animals. For it is evident that if colours which please us also attract them, and if the various disguises which have been

here enumerated are equally deceptive to them as to ourselves, then both their powers of vision and their faculties of perception and emotion, must be essentially of the same nature as our own—a fact of high philosophical importance in the study of our own nature and our true relations to the lower animals.

Conclusion.

Although such a variety of interesting facts have been already accumulated, the subject we have been discussing is one of which comparatively little is really known. The natural history of the tropics has never yet been studied on the spot with a full appreciation of “what to observe” in this matter. The varied ways in which the colouring and form of animals serve for their protection, their strange disguises as vegetable or mineral substances, their wonderful mimicry of other beings, offer an almost unworked and inexhaustible field of discovery for the zoologist, and will assuredly throw much light on the laws and conditions which have resulted in the wonderful variety of colour, shade, and marking which constitutes one of the most pleasing characteristics of the animal world, but the immediate causes of which it has hitherto been most difficult to explain.

If I have succeeded in showing that in this wide and picturesque domain of nature, results which have hitherto been supposed to depend either upon those incalculable combinations of laws which we term chance or upon the direct volition of the Creator, are

really due to the action of comparatively well-known and simple causes, I shall have attained my present purpose, which has been to extend the interest so generally felt in the more striking facts of natural history to a large class of curious but much neglected details; and to further, in however slight a degree, our knowledge of the subjection of the phenomena of life to the "Reign of Law."

IV.

THE MALAYAN PAPILIONIDÆ OR SWALLOW-TAILED BUTTERFLIES, AS ILLUSTRATIVE OF THE THEORY OF NATURAL SELECTION.

Special Value of the Diurnal Lepidoptera for enquiries of this nature.

WHEN the naturalist studies the habits, the structure, or the affinities of animals, it matters little to which group he especially devotes himself; all alike offer him endless materials for observation and research. But, for the purpose of investigating the phenomena of geographical distribution and of local, sexual, or general variation, the several groups differ greatly in their value and importance. Some have too limited a range, others are not sufficiently varied in specific forms, while, what is of most importance, many groups have not received that amount of attention over the whole region they inhabit, which could furnish materials sufficiently approaching to completeness to enable us to arrive at any accurate conclusions as to the phenomena they present as a whole. It is in those groups which are, and have long been, favourites with collectors, that the student of distribution and variation will find his materials the most satisfactory, from their comparative completeness.

Pre-eminent among such groups are the diurnal Lepidoptera or Butterflies, whose extreme beauty and endless diversity have led to their having been assiduously collected in all parts of the world, and to the numerous species and varieties having been figured in a series of magnificent works, from those of Cramer, the contemporary of Linnæus, down to the inimitable productions of our own Hewitson.* But, besides their abundance, their universal distribution, and the great attention that has been paid to them, these insects have other qualities that especially adapt them to elucidate the branches of inquiry already alluded to. These are, the immense development and peculiar structure of the wings, which not only vary in form more than those of any other insects, but offer on both surfaces an endless variety of pattern, colouring, and texture. The scales, with which they are more or less completely covered, imitate the rich hues and delicate surfaces of satin or of velvet, glitter with metallic lustre, or glow with the changeable tints of the opal. This delicately painted surface acts as a register of the minutest differences of organization—a shade of colour, an additional streak or spot, a slight modification of outline continually recurring with the greatest regularity and fixity, while the body and all its other

* W. C. Hewitson, Esq., of Oatlands, Walton-on-Thames, author of "Exotic Butterflies" and several other works, illustrated by exquisite coloured figures drawn by himself; and owner of the finest collection of Butterflies in the world.

members exhibit no appreciable change. The wings of Butterflies, as Mr. Bates has well put it, "serve as a tablet on which Nature writes the story of the modifications of species;" they enable us to perceive changes that would otherwise be uncertain and difficult of observation, and exhibit to us on an enlarged scale the effects of the climatal and other physical conditions which influence more or less profoundly the organization of every living thing.

A proof that this greater sensibility to modifying causes is not imaginary may, I think, be drawn from the consideration, that while the Lepidoptera as a whole are of all insects the least essentially varied in form, structure, or habits, yet in the number of their specific forms they are not much inferior to those orders which range over a much wider field of nature, and exhibit more deeply seated structural modifications. The Lepidoptera are all vegetable-feeders in their larva-state, and suckers of juices or other liquids in their perfect form. In their most widely separated groups they differ but little from a common type, and offer comparatively unimportant modifications of structure or of habits. The Coleoptera, the Diptera, or the Hymenoptera, on the other hand, present far greater and more essential variations. In either of these orders we have both vegetable and animal-feeders, aquatic, and terrestrial, and parasitic groups. Whole families are devoted to special departments in the economy of nature. Seeds, fruits, bones, carcasses, excrement, bark, have each their special and

dependent insect tribes from among them; whereas the Lepidoptera are, with but few exceptions, confined to the one function of devouring the foliage of living vegetation. We might therefore anticipate that their species - population would be only equal to that of sections of the other orders having a similar uniform mode of existence; and the fact that their numbers are at all comparable with those of entire orders, so much more varied in organization and habits, is, I think, a proof that they are in general highly susceptible of specific modification.

Question of the rank of the Papilionidæ.

The Papilionidæ are a family of diurnal Lepidoptera which have hitherto, by almost universal consent, held the first rank in the order; and though this position has recently been denied them, I cannot altogether acquiesce in the reasoning by which it has been proposed to degrade them to a lower rank. In Mr. Bates's most excellent paper on the Heliconidæ, (published in the Transactions of the Linnæan Society, vol. xxiii., p. 495) he claims for that family the highest position, chiefly because of the imperfect structure of the fore legs, which is there carried to an extreme degree of abortion, and thus removes them further than any other family from the Hesperidæ and Heterocera, which all have perfect legs. Now it is a question whether any amount of difference which is exhibited merely in the imperfection or abortion of certain organs, can establish in the

group exhibiting it a claim to a high grade of organization; still less can this be allowed when another group along with perfection of structure in the same organs, exhibits modifications peculiar to it, together with the possession of an organ which in the remainder of the order is altogether wanting. This is, however, the position of the Papilionidæ. The perfect insects possess two characters quite peculiar to them. Mr. Edward Doubleday, in his "Genera of Diurnal Lepidoptera," says, "The Papilionidæ may be known by the apparently four-branched median nervule and the spur on the anterior tibiæ, characters found in no other family." The four-branched median nervule is a character so constant, so peculiar, and so well marked, as to enable a person to tell, at a glance at the wings only of a butterfly, whether it does or does not belong to this family; and I am not aware that any other group of butterflies, at all comparable to this in extent and modifications of form, possesses a character in its neuration to which the same degree of certainty can be attached. The spur on the anterior tibiæ is also found in some of the Hesperidæ, and is therefore supposed to show a direct affinity between the two groups: but I do not imagine it can counterbalance the differences in neuration and in every other part of their organization. The most characteristic feature of the Papilionidæ, however, and that on which I think insufficient stress has been laid, is undoubtedly the peculiar structure of the larvæ. These all possess an extra-

ordinary organ situated on the neck, the well-known Y-shaped tentacle, which is entirely concealed in a state of repose, but which is capable of being suddenly thrown out by the insect when alarmed. When we consider this singular apparatus, which in some species is nearly half an inch long, the arrangement of muscles for its protrusion and retraction, its perfect concealment during repose, its blood-red colour, and the suddenness with which it can be thrown out, we must, I think, be led to the conclusion that it serves as a protection to the larva, by startling and frightening away some enemy when about to seize it, and is thus one of the causes which has led to the wide extension and maintained the permanence of this now dominant group. Those who believe that such peculiar structures can only have arisen by very minute successive variations, each one advantageous to its possessor, must see, in the possession of such an organ by one group, and its complete absence in every other, a proof of a very ancient origin and of very long-continued modification. And such a positive structural addition to the organization of the family, subserving an important function, seems to me alone sufficient to warrant us in considering the Papilionidæ as the most highly developed portion of the whole order, and thus in retaining it in the position which the size, strength, beauty, and general structure of the perfect insects have been generally thought to deserve.

In Mr. Trimen's paper on "Mimetic Analogies

among African Butterflies," in the Transactions of the Linnæan Society, for 1868, he has argued strongly in favour of Mr. Bates' views as to the higher position of the Danaidæ and the lower grade of the Papilionidæ, and has adduced, among other facts, the undoubted resemblance of the pupa of *Parnassius*, a genus of Papilionidæ, to that of some Hesperidæ and moths. I admit, therefore, that he has proved the Papilionidæ to have retained several characters of the nocturnal Lepidoptera which the Danaidæ have lost, but I deny that they are therefore to be considered lower in the scale of organization. Other characters may be pointed out which indicate that they are farther removed from the moths even than the Danaidæ. The club of the antennæ is the most prominent and most constant feature by which butterflies may be distinguished from moths, and of all butterflies the Papilionidæ have the most beautiful and most perfectly developed clubbed antennæ. Again, butterflies and moths are broadly characterised by their diurnal and nocturnal habits respectively, and the Papilionidæ, with their close allies the Pieridæ, are the most pre-eminently diurnal of butterflies, most of them lovers of sunshine, and not presenting a single crepuscular species. The great group of the Nymphalidæ, on the other hand (in which Mr. Bates includes the Danaidæ and Heliconidæ as sub-families), contains an entire sub-family (*Brassolidæ*) and a number of genera, such as *Thaumantis*, *Zeuxidia*, *Pavonia*, &c., of crepuscular habits, while a large

proportion of the Satyridæ and many of the Danaidæ are shade-loving butterflies. This question, of what is to be considered the highest type of any group of organisms, is one of such general interest to naturalists that it will be well to consider it a little further, by a comparison of the Lepidoptera with some groups of the higher animals.

Mr. Trimen's argument, that the lepidopterous type, like that of birds, being pre-eminently aërial, "therefore a diminution of the ambulatory organs, instead of being a sign of inferiority, may very possibly indicate a higher, because a more thoroughly aërial form," is certainly unsound, for it would imply that the most aërial of birds (the swift and the frigate-birds, for example) are the highest in the scale of bird-organization, and the more so on account of their feet being very ill adapted for walking. But no ornithologist has ever so classed them, and the claim to the highest rank among birds is only disputed between three groups, all very far removed from these. They are — 1st. The Falcons, on account of their general perfection, their rapid flight, their piercing vision, their perfect feet armed with retractile claws, the beauty of their forms, and the ease and rapidity of their motions; 2nd. The Parrots, whose feet, though ill-fitted for walking, are perfect as prehensile organs, and which possess large brains with great intelligence, though but moderate powers of flight; and, 3rd. The Thrushes or Crows, as typical of the perching birds, on account of the well-balanced development of their

whole structure, in which no organ or function has attained an undue prominence.

Turning now to the Mammalia, it might be argued that as they are pre-eminently the terrestrial type of vertebrates, to walk and run well is essential to the typical perfection of the group; but this would give the superiority to the horse, the deer, or the hunting leopard, instead of to the Quadrumana. We seem here to have quite a case in point, for one group of Quadrumana, the Lemurs, is undoubtedly nearer to the low Insectivora and Marsupials than the Carnivora or the Ungulata, as shown among other characters by the Opossums possessing a hand with perfect opposable thumb, closely resembling that of some of the Lemurs; and by the curious Galeopithecus, which is sometimes classed as a Lemur, and sometimes with the Insectivora. Again, the implacental mammals, including the Ornithodelphia and the Marsupials, are admitted to be lower than the placental series. But one of the distinguishing characters of the Marsupials is that the young are born blind and exceedingly imperfect, and it might therefore be argued that those orders in which the young are born most perfect are the highest, because farthest from the low Marsupial type. This would make the Ruminants and Ungulata higher than the Quadrumana or the Carnivora. But the Mammalia offer a still more remarkable illustration of the fallacy of this mode of reasoning, for if there is one character more than another which is essential and distinctive of the class, it is that from which it derives

its name, the possession of mammary glands and the power of suckling the young. What more reasonable, apparently, than to argue that the group in which this important function is most developed, that in which the young are most dependent upon it, and for the longest period, must be the highest in the Mammalian scale of organization? Yet this group is the Marsupial, in which the young commence suckling in a foetal condition, and continue to do so till they are fully developed, and are therefore for a long time absolutely dependent on this mode of nourishment.

These examples, I think, demonstrate that we cannot settle the rank of a group by a consideration of the degree in which certain characters resemble or differ from those in what is admitted to be a lower group; and they also show that the highest group of a class may be more closely connected to one of the lowest, than some other groups which have developed laterally and diverged farther from the parent type, but which yet, owing to want of balance or too great specialization in their structure, have never reached a high grade of organization. The *Quadrumana* afford a very valuable illustration, because, owing to their undoubted affinity with man, we feel certain that they are really higher than any other order of *Mammalia*, while at the same time they are more distinctly allied to the lowest groups than many others. The case of the *Papilionidæ* seems to me so exactly parallel to this, that, while I admit all the proofs of affinity with the undoubtedly lower groups of *Hesperidæ* and

moths, I yet maintain that, owing to the complete and even development of every part of their organization, these insects best represent the highest perfection to which the butterfly type has attained, and deserve to be placed at its head in every system of classification.

Distribution of the Papilionidæ.

The Papilionidæ are pretty widely distributed over the earth, but are especially abundant in the tropics, where they attain their maximum of size and beauty, and the greatest variety of form and colouring. South America, North India, and the Malay Islands are the regions where these fine insects occur in the greatest profusion, and where they actually become a not unimportant feature in the scenery. In the Malay Islands in particular, the giant Ornithopterae may be frequently seen about the borders of the cultivated and forest districts, their large size, stately flight, and gorgeous colouring rendering them even more conspicuous than the generality of birds. In the shady suburbs of the town of Malacca two large and handsome Papilios (Memnon and Nephelus) are not uncommon, flapping with irregular flight along the roadways, or, in the early morning, expanding their wings to the invigorating rays of the sun. In Amboyna and other towns of the Moluccas, the magnificent Deiphobus and Severus, and occasionally even the azure-winged Ulysses, frequent similar situations, fluttering about the orange-trees and flower-beds, or

sometimes even straying into the narrow bazaars or covered markets of the city. In Java the golden-dusted Arjuna may often be seen at damp places on the roadside in the mountain districts, in company with Sarpedon, Bathycles, and Agamemnon, and less frequently the beautiful swallow-tailed Antiphates. In the more luxuriant parts of these islands one can hardly take a morning's walk in the neighbourhood of a town or village without seeing three or four species of Papilio, and often twice that number. No less than 130 species of the family are now known to inhabit the Archipelago, and of these ninety-six were collected by myself. Thirty species are found in Borneo, being the largest number in any one island, twenty-three species having been obtained by myself in the vicinity of Sarawak; Java has twenty-eight species; Celebes twenty-four, and the Peninsula of Malacca, twenty-six species. Further east the numbers decrease; Batchian producing seventeen, and New Guinea only fifteen, though this number is certainly too small, owing to our present imperfect knowledge of that great island.

Definition of the word Species.

In estimating these numbers I have had the usual difficulty to encounter, of determining what to consider species and what varieties. The Malayan region, consisting of a large number of islands of generally great antiquity, possesses, compared to its actual area, a great number of distinct forms, often indeed dis-

tinguished by very slight characters, but in most cases so constant in large series of specimens, and so easily separable from each other, that I know not on what principle we can refuse to give them the name and rank of species. One of the best and most orthodox definitions is that of Pritchard, the great ethnologist, who says, that "*separate origin and distinctness of race, evinced by a constant transmission of some characteristic peculiarity of organization,*" constitutes a species. Now leaving out the question of "origin," which we cannot determine, and taking only the proof of separate origin, "*the constant transmission of some characteristic peculiarity of organization,*" we have a definition which will compel us to neglect altogether the *amount* of difference between any two forms, and to consider only whether the differences that present themselves are *permanent*. The rule, therefore, I have endeavoured to adopt is, that when the difference between two forms inhabiting separate areas seems quite constant, when it can be defined in words, and when it is not confined to a single peculiarity only, I have considered such forms to be species. When, however, the individuals of each locality vary among themselves, so as to cause the distinctions between the two forms to become inconsiderable and indefinite, or where the differences, though constant, are confined to one particular only, such as size, tint, or a single point of difference in marking or in outline, I class one of the forms as a variety of the other.

I find as a general rule that the constancy of species is in an inverse ratio to their range. Those which are confined to one or two islands are generally very constant. When they extend to many islands, considerable variability appears; and when they have an extensive range over a large part of the Archipelago, the amount of unstable variation is very large. These facts are explicable on Mr. Darwin's principles. When a species exists over a wide area, it must have had, and probably still possesses, great powers of dispersion. Under the different conditions of existence in various portions of its area, different variations from the type would be selected, and, were they completely isolated, would soon become distinctly modified forms; but this process is checked by the dispersive powers of the whole species, which leads to the more or less frequent intermixture of the incipient varieties, which thus become irregular and unstable. Where, however, a species has a limited range, it indicates less active powers of dispersion, and the process of modification under changed conditions is less interfered with. The species will therefore exist under one or more permanent forms according as portions of it have been isolated at a more or less remote period.

Laws and Modes of Variation.

What is commonly called variation consists of several distinct phenomena which have been too often confounded. I shall proceed to consider these under the heads of—1st, simple variability; 2nd, polymorphism;

3rd, local forms ; 4th, co-existing varieties ; 5th, races or subspecies ; and 6th, true species.

1. *Simple variability*.—Under this head I include all those cases in which the specific form is to some extent unstable. Throughout the whole range of the species, and even in the progeny of individuals, there occur continual and uncertain differences of form, analogous to that variability which is so characteristic of domestic breeds. It is impossible usefully to define any of these forms, because there are indefinite gradations to each other form. Species which possess these characteristics have always a wide range, and are more frequently the inhabitants of continents than of islands, though such cases are always exceptional, it being far more common for specific forms to be fixed within very narrow limits of variation. The only good example of this kind of variability which occurs among the Malayan Papilionidæ is in *Papilio Severus*, a species inhabiting all the islands of the Moluccas and New Guinea, and exhibiting in each of them a greater amount of individual difference than often serves to distinguish well-marked species. Almost equally remarkable are the variations exhibited in most of the species of *Ornithoptera*, which I have found in some cases to extend even to the form of the wing and the arrangement of the nervures. Closely allied, however, to these variable species are others which, though differing slightly from them, are constant and confined to limited areas. After satisfying oneself, by the examination of numerous specimens captured in their native countries, that the

one set of individuals are variable and the others are not, it becomes evident that by classing all alike as varieties of one species we shall be obscuring an important fact in nature; and that the only way to exhibit that fact in its true light is to treat the invariable local form as a distinct species, even though it does not offer better distinguishing characters than do the extreme forms of the variable species. Cases of this kind are the *Ornithoptera Priamus*, which is confined to the islands of Ceram and Amboyna, and is very constant in both sexes, while the allied species inhabiting New Guinea and the Papuan Islands is exceedingly variable; and in the island of Celebes is a species closely allied to the variable *P. Severus*, but which, being exceedingly constant, I have described as a distinct species under the name of *Papilio Pertinax*.

2. *Polymorphism or dimorphism*.—By this term I understand the co-existence in the same locality of two or more distinct forms, not connected by intermediate gradations, and all of which are occasionally produced from common parents. These distinct forms generally occur in the female sex only, and their offspring, instead of being hybrids, or like the two parents, appear to reproduce all the distinct forms in varying proportions. I believe it will be found that a considerable number of what have been classed as *varieties* are really cases of polymorphism. Albinoism and melanism are of this character, as well as most of those cases in which well-marked varieties occur in company with the parent species, but without any intermediate forms. If

these distinct forms breed independently, and are never reproduced from a common parent, they must be considered as separate species, contact without intermixture being a good test of specific difference. On the other hand, intercrossing without producing an intermediate race is a test of dimorphism. I consider, therefore, that under any circumstances the term "variety" is wrongly applied to such cases.

The Malayan Papilionidæ exhibit some very curious instances of polymorphism, some of which have been recorded as varieties, others as distinct species; and they all occur in the female sex. *Papilio Memnon* is one of the most striking, as it exhibits the mixture of simple variability, local and polymorphic forms, all hitherto classed under the common title of varieties. The polymorphism is strikingly exhibited by the females, one set of which resemble the males in form, with a variable paler colouring; the others have a large spatulate tail to the hinder wings and a distinct style of colouring, which causes them closely to resemble *P. Coon*, a species having the two sexes alike and inhabiting the same countries, but with which they have no direct affinity. The tailless females exhibit simple variability, scarcely two being found exactly alike even in the same locality. The males of the island of Borneo exhibit constant differences of the under surface, and may therefore be distinguished as a local form, while the continental specimens, as a whole, offer such large and constant differences from those of the islands, that I am inclined to separate them as a distinct species, to

which the name *P. Androgeus* (Cramer) may be applied. We have here, therefore, distinct species, local forms, polymorphism, and simple variability, which seem to me to be distinct phenomena, but which have been hitherto all classed together as varieties. I may mention that the fact of these distinct forms being one species is doubly proved. The males, the tailed and tailless females, have all been bred from a single group of the larvæ, by Messrs. Payen and Bocarmé, in Java, and I myself captured, in Sumatra, a male *P. Memnon*, and a tailed female *P. Achates*, under circumstances which led me to class them as the same species.

Papilio Pammon offers a somewhat similar case. The female was described by Linnæus as *P. Polytes*, and was considered to be a distinct species till Westermann bred the two from the same larvæ (see Boisduval, "*Species Général des Lépidoptères*," p. 272). They were therefore classed as sexes of one species by Mr. Edward Doubleday, in his "*Genera of Diurnal Lepidoptera*," in 1846. Later, female specimens were received from India closely resembling the male insect, and this was held to overthrow the authority of M. Westermann's observation, and to re-establish *P. Polytes* as a distinct species; and as such it accordingly appears in the British Museum List of *Papilionidæ* in 1856, and in the Catalogue of the East India Museum in 1857. This discrepancy is explained by the fact of *P. Pammon* having two females, one closely resembling the male, while the other is totally different from it. A long familiarity with this insect (which

replaced by local forms or by closely allied species, occurs in every island of the Archipelago) has convinced me of the correctness of this statement; for in every place where a male allied to *P. Pammon* is found, a female resembling *P. Polytes* also occurs, and sometimes, though less frequently than on the continent, another female closely resembling the male: while not only has no male specimen of *P. Polytes* yet been discovered, but the female (*Polytes*) has never yet been found in localities to which the male (*Pammon*) does not extend. In this case, as in the last, distinct species, local forms, and dimorphic specimens, have been confounded under the common appellation of varieties.

But, besides the true *P. Polytes*, there are several allied forms of females to be considered, namely, *P. Theseus* (Cramer), *P. Melanides* (De Haan), *P. Elyros* (G. R. Gray), and *P. Romulus* (Linnæus). The dark female figured by Cramer as *P. Theseus* seems to be the common and perhaps the only form in Sumatra, whereas in Java, Borneo, and Timor, along with males quite identical with those of Sumatra, occur females of the *Polytes* form, although a single specimen of the true *P. Theseus* taken at Lombock would seem to show that the two forms do occur together. In the allied species found in the Philippine Islands (*P. Alphenor*, Cramer = *P. Ledebouria*, Eschscholtz, the female of which is *P. Elyros*, G. R. Gray,) forms corresponding to these extremes occur, along with a number of intermediate varieties, as shown by a fine series in the British Museum. We have here an

indication of how dimorphism may be produced; for let the extreme Philippine forms be better suited to their conditions of existence than the intermediate connecting links, and the latter will gradually die out, leaving two distinct forms of the same insect, each adapted to some special conditions. As these conditions are sure to vary in different districts, it will often happen, as in Sumatra and Java, that the one form will predominate in the one island, the other in the adjacent one. In the island of Borneo there seems to be a third form; for *P. Melanides* (De Haan) evidently belongs to this group, and has all the chief characteristics of *P. Theseus*, with a modified colouration of the hind wings. I now come to an insect which, if I am correct, offers one of the most interesting cases of variation yet adduced. *Papilio Romulus*, a butterfly found over a large part of India and Ceylon, and not uncommon in collections, has always been considered a true and independent species, and no suspicions have been expressed regarding it. But a male of this form does not, I believe, exist. I have examined the fine series in the British Museum, in the East India Company's Museum, in the Hope Museum at Oxford, in Mr. Hewitson's and several other private collections, and can find nothing but females; and for this common butterfly no male partner can be found except the equally common *P. Pammon*, a species already provided with two wives, and yet to whom we shall be forced, I believe, to assign a third. On carefully examining *P. Romulus*,

I find that in all essential characters—the form and texture of the wings, the length of the antennæ, the spotting of the head and thorax, and even the peculiar tints and shades with which it is ornamented—it corresponds exactly with the other females of the Pammon group; and though, from the peculiar marking of the fore wings, it has at first sight a very different aspect, yet a closer examination shows that every one of its markings could be produced by slight and almost imperceptible modifications of the various allied forms. I fully believe, therefore, that I shall be correct in placing *P. Romulus* as a third Indian form of the female *P. Pammon*, corresponding to *P. Melanides*, the third form of the Malayan *P. Theseus*. I may mention here that the females of this group have a superficial resemblance to the *Polydorus* group of *Papilios*, as shown by *P. Theseus* having been considered to be the female of *P. Antiphus*, and by *P. Romulus* being arranged next to *P. Hector*. There is no close affinity between these two groups of *Papilio*, and I am disposed to believe that we have here a case of mimicry, brought about by the same causes which Mr. Bates has so well explained in his account of the *Heliconidæ*, and which has led to the singular exuberance of polymorphic forms in this and allied groups of the genus *Papilio*. I shall have to devote a section of my essay to the consideration of this subject.

The third example of polymorphism I have to bring forward is *Papilio Ormenus*, which is closely allied

to the well-known *P. Erechtheus*, of Australia. The most common form of the female also resembles that of *P. Erechtheus*; but a totally different-looking insect was found by myself in the Aru Islands, and figured by Mr. Hewitson under the name of *P. Onesimus*, which subsequent observation has convinced me is a second form of the female of *P. Ormenus*. Comparison of this with Boisduval's description of *P. Amanga*, a specimen of which from New Guinea is in the Paris Museum, shows the latter to be a closely similar form; and two other specimens were obtained by myself, one in the island of Goram and the other in Waigiou, all evidently local modifications of the same form. In each of these localities males and ordinary females of *P. Ormenus* were also found. So far there is no evidence that these light-coloured insects are not females of a distinct species, the males of which have not been discovered. But two facts have convinced me this is not the case. At Dorey, in New Guinea, where males and ordinary females closely allied to *P. Ormenus* occur (but which seem to me worthy of being separated as a distinct species), I found one of these light-coloured females closely followed in her flight by three males, exactly in the same manner as occurs (and, I believe, occurs only) with the sexes of the same species. After watching them a considerable time, I captured the whole of them, and became satisfied that I had discovered the true relations of this anomalous form. The next year I had corroborative proof of the correctness of this opinion

by the discovery in the island of Batchian of a new species allied to *P. Ormenus*, all the females of which, either seen or captured by me, were of one form, and much more closely resembling the abnormal light-coloured females of *P. Ormenus* and *P. Pandion* than the ordinary specimens of that sex. Every naturalist will, I think, agree that this is strongly confirmative of the supposition that both forms of female are of one species; and when we consider, further, that in four separate islands, in each of which I resided for several months, the two forms of female were obtained and only one form of male ever seen, and that about the same time, M. Montrouzier in Woodlark Island, at the other extremity of New Guinea (where he resided several years, and must have obtained all the large Lepidoptera of the island), obtained females closely resembling mine, which, in despair at finding no appropriate partners for them, he mates with a widely different species—it becomes, I think, sufficiently evident this is another case of polymorphism of the same nature as those already pointed out in *P. Pammon* and *P. Memnon*. This species, however, is not only dimorphic, but trimorphic; for, in the island of Waigiou, I obtained a third female quite distinct from either of the others, and in some degree intermediate between the ordinary female and the male. The specimen is particularly interesting to those who believe, with Mr. Darwin, that extreme difference of the sexes has been gradually produced by what he terms sexual selection, since it may be

supposed to exhibit one of the intermediate steps in that process, which has been accidentally preserved in company with its more favoured rivals, though its extreme rarity (only one specimen having been seen to many hundreds of the other form) would indicate that it may soon become extinct.

The only other case of polymorphism in the genus *Papilio*, at all equal in interest to those I have now brought forward, occurs in America; and we have, fortunately, accurate information about it. *Papilio Turnus* is common over almost the whole of temperate North America; and the female resembles the male very closely. A totally different-looking insect both in form and colour, *Papilio Glaucus*, inhabits the same region; and though, down to the time when Boisduval published his "*Species Général*," no connexion was supposed to exist between the two species, it is now well ascertained that *P. Glaucus* is a second female form of *P. Turnus*. In the "*Proceedings of the Entomological Society of Philadelphia*," Jan., 1863, Mr. Walsh gives a very interesting account of the distribution of this species. He tells us that in the New England States and in New York all the females are yellow, while in Illinois and further south all are black; in the intermediate region both black and yellow females occur in varying proportions. Lat. 37° is approximately the southern limit of the yellow form, and 42° the northern limit of the black form; and, to render the proof complete, both black and yellow insects have been bred from a single batch

of eggs. He further states that, out of thousands of specimens, he has never seen or heard of intermediate varieties between these forms. In this interesting example we see the effects of latitude in determining the proportions in which the individuals of each form should exist. The conditions are *here* favourable to the one form, *there* to the other; but we are by no means to suppose that these conditions consist in climate alone. It is highly probable that the existence of enemies, and of competing forms of life, may be the main determining influences; and it is much to be wished that such a competent observer as Mr. Walsh would endeavour to ascertain what are the adverse causes which are most efficient in keeping down the numbers of each of these contrasted forms.

Dimorphism of this kind in the animal kingdom does not seem to have any direct relations to the reproductive powers, as Mr. Darwin has shown to be the case in plants, nor does it appear to be very general. One other case only is known to me in another family of my eastern Lepidoptera, the Pieridæ; and but few occur in the Lepidoptera of other countries. The spring and autumn broods of some European species differ very remarkably; and this must be considered as a phenomenon of an analogous though not of an identical nature, while the *Araschnia prorsa*, of Central Europe, is a striking example of this alternate or seasonal dimorphism. Among our nocturnal Lepidoptera, I am informed,

many analogous cases occur; and as the whole history of many of these has been investigated by breeding successive generations from the egg, it is to be hoped that some of our British Lepidopterists will give us a connected account of all the abnormal phenomena which they present. Among the Coleoptera Mr. Pascoe has pointed out the existence of two forms of the male sex in seven species of the two genera *Xenocerus* and *Mecocerus* belonging to the family Anthribidæ, (Proc. Ent. Soc. Lond., 1862); and no less than six European Water-beetles, of the genus *Dytiscus*, have females of two forms, the most common having the elytra deeply sulcate, the rarer smooth as in the males. The three, and sometimes four or more, forms under which many Hymenopterous insects (especially Ants) occur, must be considered as a related phenomenon, though here each form is specialized to a distinct function in the economy of the species. Among the higher animals, albinism and melanism may, as I have already stated, be considered as analogous facts; and I met with one case of a bird, a species of Lory (*Eos fuscata*), clearly existing under two differently coloured forms, since I obtained both sexes of each from a single flock, while no intermediate specimens have yet been found.

The fact of the two sexes of one species differing very considerably is so common, that it attracted but little attention till Mr. Darwin showed how it could in many cases be explained by the principle of

sexual selection. For instance, in most polygamous animals the males fight for the possession of the females, and the victors, always becoming the progenitors of the succeeding generation, impress upon their male offspring their own superior size, strength, or unusually developed offensive weapons. It is thus that we can account for the spurs and the superior strength and size of the males in Gallinaceous birds, and also for the large canine tusks in the males of fruit-eating Apes. So the superior beauty of plumage and special adornments of the males of so many birds can be explained by supposing (what there are many facts to prove) that the females prefer the most beautiful and perfect-plumaged males, and that thus, slight accidental variations of form and colour have been accumulated, till they have produced the wonderful train of the Peacock and the gorgeous plumage of the Bird of Paradise. Both these causes have no doubt acted partially in insects, so many species possessing horns and powerful jaws in the male sex only, and still more frequently the males alone rejoicing in rich colours or sparkling lustre. But there is here another cause which has led to sexual differences, viz., a special adaptation of the sexes to diverse habits or modes of life. This is well seen in female Butterflies (which are generally weaker and of slower flight), often having colours better adapted to concealment; and in certain South American species (*Papilio torquatus*) the females, which inhabit the forests, resemble the *Æneas* group of *Papilios* which abound

in similar localities, while the males, which frequent the sunny open river-banks, have a totally different colouration. In these cases, therefore, natural selection seems to have acted independently of sexual selection; and all such cases may be considered as examples of the simplest dimorphism, since the offspring never offer intermediate varieties between the parent forms.

The phenomena of dimorphism and polymorphism may be well illustrated by supposing that a blue-eyed, flaxen-haired Saxon man had two wives, one a black-haired, red-skinned Indian squaw, the other a woolly-headed, sooty-skinned negress—and that instead of the children being mulattoes of brown or dusky tints, mingling the separate characteristics of their parents in varying degrees, all the boys should be pure Saxon boys like their father, while the girls should altogether resemble their mothers. This would be thought a sufficiently wonderful fact; yet the phenomena here brought forward as existing in the insect-world are still more extraordinary; for each mother is capable not only of producing male offspring like the father, and female like herself, but also of producing other females exactly like her fellow-wife, and altogether differing from herself. If an island could be stocked with a colony of human beings having similar physiological idiosyncrasies with *Papilio Pammon* or *Papilio Ormenus*, we should see white men living with yellow, red, and black women, and their offspring always reproducing the same types; so that

at the end of many generations the men would remain pure white, and the women of the same well-marked races as at the commencement.

The distinctive character therefore of dimorphism is this, that the union of these distinct forms does not produce intermediate varieties, but reproduces the distinct forms unchanged. In simple varieties, on the other hand, as well as when distinct local forms or distinct species are crossed, the offspring never resembles either parent exactly, but is more or less intermediate between them. Dimorphism is thus seen to be a specialized result of variation, by which new physiological phenomena have been developed; the two should therefore, whenever possible, be kept separate.

3. *Local form, or variety.*—This is the first step in the transition from variety to species. It occurs in species of wide range, when groups of individuals have become partially isolated in several points of its area of distribution, in each of which a characteristic form has become more or less completely segregated. Such forms are very common in all parts of the world, and have often been classed by one author as varieties, by another as species. I restrict the term to those cases where the difference of the forms is very slight, or where the segregation is more or less imperfect. The best example in the present group is *Papilio Agamemnon*, a species which ranges over the greater part of tropical Asia, the whole of the Malay archipelago, and a portion of the Australian and Pacific regions. The modifications are principally of size and form,

and, though slight, are tolerably constant in each locality. The steps, however, are so numerous and gradual that it would be impossible to define many of them, though the extreme forms are sufficiently distinct. *Papilio Sarpedon* presents somewhat similar but less numerous variations.

4. *Co-existing Variety*.—This is a somewhat doubtful case. It is when a slight but permanent and hereditary modification of form exists in company with the parent or typical form, without presenting those intermediate gradations which would constitute it a case of simple variability. It is evidently only by direct evidence of the two forms breeding separately that this can be distinguished from dimorphism. The difficulty occurs in *Papilio Jason*, and *P. Evemon*, which inhabit the same localities, and are almost exactly alike in form, size, and colouration, except that the latter always wants a very conspicuous red spot on the under surface, which is found not only in *P. Jason*, but in all the allied species. It is only by breeding the two insects that it can be determined whether this is a case of a co-existing variety or of dimorphism. In the former case, however, the difference being constant and so very conspicuous and easily defined, I see not how we could escape considering it as a distinct species. A true case of co-existing forms would, I consider, be produced, if a slight variety had become fixed as a local form, and afterwards been brought into contact with the parent species, with little or no intermixture of the two; and such instances do very probably occur.

5. *Race or subspecies.*—These are local forms completely fixed and isolated; and there is no possible test but individual opinion to determine which of them shall be considered as species and which varieties. If stability of form and “*the constant transmission of some characteristic peculiarity of organization*” is the test of a species (and I can find no other test that is more certain than individual opinion) then every one of these fixed races, confined as they almost always are to distinct and limited areas, must be regarded as a species; and as such I have in most cases treated them. The various modifications of *Papilio Ulysses*, *P. Peranthus*, *P. Codrus*, *P. Eurypilus*, *P. Helenus*, &c., are excellent examples; for while some present great and well-marked, others offer slight and inconspicuous differences, yet in all cases these differences seem equally fixed and permanent. If, therefore, we call some of these forms species, and others varieties, we introduce a purely arbitrary distinction, and shall never be able to decide where to draw the line. The races of *Papilio Ulysses*, for example, vary in amount of modification from the scarcely differing New Guinea form to those of Woodlark Island and New Caledonia, but all seem equally constant; and as most of these had already been named and described as species, I have added the New Guinea form under the name of *P. Autolytus*. We thus get a little group of Ulyssine *Papilios*, the whole comprised within a very limited area, each one confined to a separate portion of that area, and, though differing in various amounts, each apparently constant.

Few naturalists will doubt that all these may and probably have been derived from a common stock, and therefore it seems desirable that there should be a unity in our method of treating them; either call them all *varieties* or all *species*. Varieties, however, continually get overlooked; in lists of species they are often altogether unrecorded; and thus we are in danger of neglecting the interesting phenomena of variation and distribution which they present. I think it advisable, therefore, to name all such forms; and those who will not accept them as species may consider them as subspecies or races.

6. *Species*. — Species are merely those strongly marked races or local forms which when in contact do not intermix, and when inhabiting distinct areas are generally believed to have had a separate origin, and to be incapable of producing a fertile hybrid offspring. But as the test of hybridity cannot be applied in one case in ten thousand, and even if it could be applied would prove nothing, since it is founded on an assumption of the very question to be decided—and as the test of separate origin is in every case inapplicable—and as, further, the test of non-intermixture is useless, except in those rare cases where the most closely allied species are found inhabiting the same area, it will be evident that we have no means whatever of distinguishing so-called “true species” from the several modes of variation here pointed out, and into which they so often pass by an insensible gradation. It is quite true that, in

the great majority of cases, what we term "species" are so well marked and definite that there is no difference of opinion about them; but as the test of a true theory is, that it accounts for, or at the very least is not inconsistent with, the whole of the phenomena and apparent anomalies of the problem to be solved, it is reasonable to ask that those who deny the origin of species by variation and selection should grapple with the facts in detail, and show how the doctrine of the distinct origin and permanence of species will explain and harmonize them. It has been recently asserted by Dr. J. E. Gray (in the Proceedings of the Zoological Society for 1863, page 134), that the difficulty of limiting species is in proportion to our ignorance, and that just as groups or countries are more accurately known and studied in greater detail the limits of species become settled. This statement has, like many other general assertions, its portion of both truth and error. There is no doubt that many uncertain species, founded on few or isolated specimens, have had their true nature determined by the study of a good series of examples: they have been thereby established as species or as varieties; and the number of times this has occurred is doubtless very great. But there are other, and equally trustworthy cases, in which, not single species, but whole groups have, by the study of a vast accumulation of materials, been proved to have no definite specific limits. A few of these must be adduced. In Dr. Carpenter's "Introduction to the Study of the Fora-

minifera," he states that "*there is not a single specimen of plant or animal of which the range of variation has been studied by the collocation and comparison of so large a number of specimens as have passed under the review of Messrs. Williamson, Parker, Rupert Jones, and myself, in our studies of the types of this group;*" and the result of this extended comparison of specimens is stated to be, "*The range of variation is so great among the Foraminifera as to include not merely those differential characters which have been usually accounted SPECIFIC, but also those upon which the greater part of the GENERA of this group have been founded, and even in some instances those of its ORDERS*" (Foraminifera, Preface, x). Yet this same group had been divided by D'Orbigny and other authors into a number of clearly defined *families, genera, and species*, which these careful and conscientious researches have shown to have been almost all founded on incomplete knowledge.

Professor DeCandolle has recently given the results of an extensive review of the species of Cupuliferæ. He finds that the best-known species of oaks are those which produce most varieties and subvarieties; that they are often surrounded by provisional species; and, with the fullest materials at his command, two-thirds of the species he considers more or less doubtful. His general conclusion is, that "*in botany the lowest series of groups, SUBVARIETIES, VARIETIES, and RACES are very badly limited; these can be grouped into SPECIES a little less vaguely limited, which again can be formed into sufficiently precise GENERA.*" This

general conclusion is entirely objected to by the writer of the article in the "Natural History Review," who, however, does not deny its applicability to the particular order under discussion, while this very difference of opinion is another proof that difficulties in the determination of species do not, any more than in the higher groups, vanish with increasing materials and more accurate research.

Another striking example of the same kind is seen in the genera *Rubus* and *Rosa*, adduced by Mr. Darwin himself; for though the amplest materials exist for a knowledge of these groups, and the most careful research has been bestowed upon them, yet the various species have not thereby been accurately limited and defined so as to satisfy the majority of botanists. In Mr. Baker's revision of the British Roses, just published by the Linnæan Society, the author includes under the single species *Rosa canina*, no less than twenty-eight named *varieties*, distinguished by more or less constant characters and often confined to special localities; and to these are referred about seventy of the *species* of Continental and British botanists.

Dr. Hooker seems to have found the same thing in his study of the Arctic flora. For though he has had much of the accumulated materials of his predecessors to work upon, he continually expresses himself as unable to do more than group the numerous and apparently fluctuating forms into more or less imperfectly defined species. In his paper on the "Dis-

tribution of Arctic Plants," (Trans. Linn. Soc. xxiii., p. 310) Dr. Hooker says:—"The most able and experienced descriptive botanists vary in their estimate of the value of the 'specific term' to a much greater extent than is generally supposed." . . . "I think I may safely affirm that the 'specific term' has three different standard values, all current in descriptive botany, but each more or less confined to one class of observers." . . . "This is no question of what is right or wrong as to the real value of the specific term; I believe each is right according to the standard he assumes as the specific."

Lastly, I will adduce Mr. Bates's researches on the Amazons. During eleven years he accumulated vast materials, and carefully studied the variation and distribution of insects. Yet he has shown that many species of Lepidoptera, which before offered no special difficulties, are in reality most intricately combined in a tangled web of affinities, leading by such gradual steps from the slightest and least stable variations to fixed races and well-marked species, that it is very often impossible to draw those sharp dividing-lines which it is supposed that a careful study and full materials will always enable us to do.

These few examples show, I think, that in every department of nature there occur instances of the instability of specific form, which the increase of materials aggravates rather than diminishes. And it must be remembered that the naturalist is rarely likely to err on the side of imputing greater indefiniteness to

species than really exists. There is a completeness and satisfaction to the mind in defining and limiting and naming a species, which leads us all to do so whenever we conscientiously can, and which we know has led many collectors to reject vague intermediate forms as destroying the symmetry of their cabinets. We must therefore consider these cases of excessive variation and instability as being thoroughly well established; and to the objection that, after all, these cases are but few compared with those in which species can be limited and defined, and are therefore merely exceptions to a general rule, I reply that a true law embraces all apparent exceptions, and that to the great laws of nature there are no real exceptions—that what appear to be such are equally results of law, and are often (perhaps indeed always) those very results which are most important as revealing the true nature and action of the law. It is for such reasons that naturalists now look upon the study of *varieties* as more important than that of well-fixed species. It is in the former that we see nature still at work, in the very act of producing those wonderful modifications of form, that endless variety of colour, and that complicated harmony of relations, which gratify every sense and give occupation to every faculty of the true lover of nature.

Variation as specially influenced by Locality.

The phenomena of variation as influenced by locality have not hitherto received much attention. Botanists,

it is true, are acquainted with the influences of climate, altitude, and other physical conditions, in modifying the forms and external characteristics of plants; but I am not aware that any peculiar influence has been traced to locality, independent of climate. Almost the only case I can find recorded is mentioned in that repertory of natural-history facts, "The Origin of Species," viz. that herbaceous groups have a tendency to become arboreal in islands. In the animal world, I cannot find that any facts have been pointed out as showing the special influence of locality in giving a peculiar *facies* to the several disconnected species that inhabit it. What I have to adduce on this matter will therefore, I hope, possess some interest and novelty.

On examining the closely allied species, local forms, and varieties distributed over the Indian and Malayan regions, I find that larger or smaller districts, or even single islands, give a special character to the majority of their Papilionidæ. For instance: 1. The species of the Indian region (Sumatra, Java, and Borneo) are almost invariably smaller than the allied species inhabiting Celebes and the Moluccas; 2. The species of New Guinea and Australia are also, though in a less degree, smaller than the nearest species or varieties of the Moluccas; 3. In the Moluccas themselves the species of Amboyna are the largest; 4. The species of Celebes equal or even surpass in size those of Amboyna; 5. The species and varieties of Celebes possess a striking character in the form of

the anterior wings, different from that of the allied species and varieties of all the surrounding islands; 6. Tailed species in India or the Indian region become tailless as they spread eastward through the archipelago; 7. In Amboyna and Ceram the females of several species are dull-coloured, while in the adjacent islands they are more brilliant.

Local variation of Size.—Having preserved the finest and largest specimens of Butterflies in my own collection, and having always taken for comparison the largest specimens of the same sex, I believe that the tables I now give are sufficiently exact. The differences of expanse of wings are in most cases very great, and are much more conspicuous in the specimens themselves than on paper. It will be seen that no less than fourteen Papilionidæ inhabiting Celebes and the Moluccas are from one-third to one-half greater in extent of wing than the allied species representing them in Java, Sumatra, and Borneo. Six species inhabiting Amboyna are larger than the closely allied forms of the northern Moluccas and New Guinea by about one-sixth. These include almost every case in which closely allied species can be compared.

Species of Papilionidæ of the Moluccas and Celebes (large).		Closely allied species of Java and the Indian region (small).	
	Expanse. Inches.		Expanse. Inches.
Ornithoptera Helena		}	O. Pompeus 5·8
Amboyna)	7·6		O. Amphrisius 6·0
Papilio Adamantius		}	P. Peranthus 3·8
(Celebes)	5·8		
P. Lorquinianus (Mo- luccas)	4·8		

Species of Papilionidæ of the Moluccas and Celebes (large).

	Expanse. Inches.
P. Blumei (Celebes) ...	5·4
P. Alphenor (Celebes)...	4·8
P. Gigon (Celebes) ...	5·4
P. Deucalion (Celebes)...	4·6
P. Agamemnon, var. (Celebes)	4·4
P. Eurypilus (Moluccas)	4·0
P. Telephus (Celebes)...	4·3
P. Ægisthus (Moluccas)	4·4
P. Milon (Celebes) ...	4·4
P. Androcles (Celebes)...	4·8
P. Polyphontes (Celebes)	4·6
Leptocircus Ennius (Celebes)	2·0

Species inhabiting Amboyna (large).

Papilio Ulysses	6·1
P. Polydorus... ..	4·9
P. Deiphobus	6·8
P. Gambrisius	6·4
P. Codrus	5·1
Ornithoptera Priamus, (male)	8·3

Closely allied species of Java and the Indian region (small).

	Expanse. Inches.
P. Brama	4·0
P. Theseus	3·6
P. Demolion	4·0
P. Macareus	3·7
P. Agamemnon, var. ...	3·8
P. Jason... ..	3·4
P. Rama... ..	3·2
P. Sarpedon	3·8
P. Antiphates	3·7
P. Diphilus	3·9
L. Meges	1·8

Allied species of New Guinea and the North Moluccas (smaller).

P. Autolyceus	5·2
P. Telegonus... ..	4·0
P. Leodamas... ..	4·0
P. Deiphontes	5·8
P. Ormenus	5·6
P. Tydeus	6·0
P. Codrus, var. papu- ensis	4·3
Ornithoptera Poseidon, (male)	7·0

Local variation of Form.—The differences of form are equally clear. Papilio Pammon everywhere on the continent is tailed in both sexes. In Java, Sumatra, and Borneo, the closely allied P. Theseus has a very short tail, or tooth only, in the male, while in the females the tail is retained. Further east, in Celebes and the South Moluccas, the hardly separable P. Alphenor has quite

lost the tail in the male, while the female retains it, but in a narrower and less spatulate form. A little further, in Gilolo, *P. Nicanor* has completely lost the tail in both sexes.

Papilio Agamemnon exhibits a somewhat similar series of changes. In India it is always tailed; in the greater part of the archipelago it has a very short tail; while far east, in New Guinea and the adjacent islands, the tail has almost entirely disappeared.

In the *Polydorus*-group two species, *P. Antiphus* and *P. Diphilus*, inhabiting India and the Indian region, are tailed, while the two which take their place in the Moluccas, New Guinea, and Australia, *P. Polydorus* and *P. Leodamas*, are destitute of tail, the species furthest east having lost this ornament the most completely.

Western species, Tailed.	Allied Eastern species not Tailed.
<i>Papilio Pammon</i> (India) ...	<i>P. Thesus</i> (Islands) minute tail.
<i>P. Agamemnon</i> , var. (India)	<i>P. Agamemnon</i> , var. (Islands).
<i>P. Antiphus</i> (India, Java) ...	<i>P. Polydorus</i> (Moluccas).
<i>P. Diphilus</i> (India, Java) ...	<i>P. Leodamas</i> (New Guinea).

The most conspicuous instance of local modification of form, however, is exhibited in the island of Celebes, which in this respect, as in some others, stands alone and isolated in the whole archipelago. Almost every species of *Papilio* inhabiting Celebes has the wings of a peculiar shape, which distinguishes them at a glance from the allied species of every other island. This peculiarity consists, first, in the upper wings being generally more elongate and falcate; and se-

condly, in the costa or anterior margin being much more curved, and in most instances exhibiting near the base an abrupt bend or elbow, which in some species is very conspicuous. This peculiarity is visible, not only when the Celebesian species are compared with their small-sized allies of Java and Borneo, but also, and in an almost equal degree, when the large forms of Amboyna and the Moluccas are the objects of comparison, showing that this is quite a distinct phenomenon from the difference of size which has just been pointed out.

In the following Table I have arranged the chief Papilios of Celebes in the order in which they exhibit this characteristic form most prominently.

Papilios of Celebes, having the wings falcate or with abruptly curved costa.	Closely allied Papilios of the surrounding islands, with less falcate wings and slightly curved costa.
1. P. Gigon	P. Demolion (Java).
2. P. Pamphylus	P. Jason (Sumatra).
3. P. Milon	P. Sarpedon (Moluccas, Java).
4. P. Agamemnon, var.	P. Agamemnon, var. (Borneo).
5. P. Adamantius	P. Peranthus (Java).
6. P. Ascalaphus	P. Deiphontes (Gilolo).
7. P. Sataspes	P. Helenus (Java).
8. P. Blumei	P. Brama (Sumatra).
9. P. Androcles	P. Antiphates (Borneo).
10. P. Rhesus	P. Aristæus (Moluccas).
11. P. Theseus, var. (male)	P. Thesus (male) (Java).
12. P. Codrus, var.	P. Codrus (Moluccas).
13. P. Encelades	P. Leucothoë (Malacca).

It thus appears that every species of Papilio exhibits this peculiar form in a greater or less degree, except one, P. Polyphontes, allied to P. Diphilus of India

and *P. Polydorus* of the Moluccas. This fact I shall recur to again, as I think it helps us to understand something of the causes that may have brought about the phenomenon we are considering. Neither do the genera *Ornithoptera* and *Leptocircus* exhibit any traces of this peculiar form. In several other families of Butterflies this characteristic form reappears in a few species. In the *Pieridæ* the following species, all peculiar to Celebes, exhibit it distinctly:—

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|----------------------------------|-----|---|
| 1. <i>Pieris Eperia</i> ... | ... | compared with <i>P. Coronis</i> (Java). |
| 2. <i>Thyca Zebuda</i> ... | ... | „ „ <i>Thyca Descombesi</i>
(India). |
| 3. <i>T. Rosenbergii</i> ... | ... | „ „ <i>T. Hyparete</i> (Java). |
| 4. <i>Tachyris Hombronii</i> ... | ... | „ „ <i>T. Lyncida</i> . |
| 5. <i>T. Lycaste</i> ... | ... | „ „ <i>T. Lyncida</i> . |
| 6. <i>T. Zarinda</i> ... | ... | „ „ <i>T. Nero</i> (Malacca). |
| 7. <i>T. Ithome</i> ... | ... | „ „ <i>T. Nephele</i> . |
| 8. <i>Eronia tritæa</i> ... | ... | „ „ <i>Ercnia Valeria</i>
(Java). |
| 9 <i>Iphias Glaucippe</i> , var. | „ | „ <i>Iphias Glaucippe</i>
(Java). |

The species of *Terias*, one or two *Pieris*, and the genus *Callidryas* do not exhibit any perceptible change of form.

In the other families there are but few similar examples. The following are all that I can find in my collection:—

- | | | |
|-------------------------------|-----|---|
| <i>Cethosia Æole</i> ... | ... | compared with <i>Cethosia Biblis</i> (Java). |
| <i>Eurhinia megalonice</i> | „ | „ <i>Eurhinia Polynice</i>
(Borneo). |
| <i>Limenitis Limire</i> ... | „ | „ <i>Limenitis Procris</i>
(Java). |
| <i>Cynthia Arsinoë</i> , var. | „ | „ <i>Cynthia Arsinoë</i> (Java,
Sumatra, Borneo) |

All these belong to the family of the Nymphalidæ. Many other genera of this family, as *Diadema*, *Adolias*, *Charaxes*, and *Cyrestis*, as well as the entire families of the *Danaidæ*, *Satyridæ*, *Lycænidæ*, and *Hesperidæ*, present no examples of this peculiar form of the upper wing in the Celebesian species.

Local variations of Colour.—In Amboyna and Ceram the female of the large and handsome Ornithoptera *Helena* has the large patch on the hind wings constantly of a pale dull ochre or buff colour, while in the scarcely distinguishable varieties from the adjacent islands of Bouru and New Guinea, it is of a golden yellow, hardly inferior in brilliancy to its colour in the male sex. The female of Ornithoptera *Priamus* (inhabiting Amboyna and Ceram exclusively) is of a pale dusky brown tint, while in all the allied species the same sex is nearly black with contrasted white markings. As a third example, the female of *Papilio Ulysses* has the blue colour obscured by dull and dusky tints, while in the closely allied species from the surrounding islands, the females are of almost as brilliant an azure blue as the males. A parallel case to this is the occurrence, in the small islands of Goram, Matabello, Ké, and Aru, of several distinct species of *Euplæa* and *Diadema*, having broad bands or patches of white, which do not exist in any of the allied species from the larger islands. These facts seem to indicate some local influence in modifying colour, as unintelligible and almost as remarkable as that which has resulted in the modifications of form previously described.

Remarks on the facts of Local variation.

The facts now brought forward seem to me of the highest interest. We see that almost all the species in two important families of the Lepidoptera (Papilionidæ and Pieridæ) acquire, in a single island, a characteristic modification of form distinguishing them from the allied species and varieties of all the surrounding islands. In other equally extensive families no such change occurs, except in one or two isolated species. However we may account for these phenomena, or whether we may be quite unable to account for them, they furnish, in my opinion, a strong corroborative testimony in favour of the doctrine of the origin of species by successive small variations; for we have here slight varieties, local races, and undoubted species, all modified in exactly the same manner, indicating plainly a common cause producing identical results. On the generally received theory of the original distinctness and permanence of species, we are met by this difficulty: one portion of these curiously modified forms are admitted to have been produced by variation and some natural action of local conditions; whilst the other portion, differing from the former only in degree, and connected with them by insensible gradations, are said to have possessed this peculiarity of form at their first creation, or to have derived it from unknown causes of a totally distinct nature. Is not the *à priori* evidence in favour of an identity of the causes that have produced such

similar results? and have we not a right to call upon our opponents for some proofs of their own doctrine, and for an explanation of its difficulties, instead of their assuming that they are right, and laying upon us the burthen of disproof?

Let us now see if the facts in question do not themselves furnish some clue to their explanation. Mr. Bates has shown that certain groups of butterflies have a defence against insectivorous animals, independent of swiftness of motion. These are generally very abundant, slow, and weak fliers, and are more or less the objects of mimicry by other groups, which thus gain an advantage in a freedom from persecution similar to that enjoyed by those they resemble. Now the only *Papilios* which have not in Celebes acquired the peculiar form of wing, belong to a group which is imitated both by other species of *Papilio* and by Moths of the genus *Epicopeia*. This group is of weak and slow flight; and we may therefore fairly conclude that it possesses some means of defence (probably in a peculiar odour or taste) which saves it from attack. Now the arched costa and falcate form of wing is generally supposed to give increased powers of flight, or, as seems to me more probable, greater facility in making sudden turnings, and thus baffling a pursuer. But the members of the *Polydorus*-group (to which belongs the only unchanged Celebesian *Papilio*), being already guarded against attack, have no need of this increased power of wing; and "natural selection" would therefore have no tendency to produce it. The whole family

of Danaidæ are in the same position: they are slow and weak fliers; yet they abound in species and individuals, and are the objects of mimicry. The Satyridæ have also probably a means of protection—perhaps their keeping always near the ground and their generally obscure colours; while the Lycænidæ and Hesperidæ may find security in their small size and rapid motions. In the extensive family of the Nymphalidæ, however, we find that several of the larger species, of comparatively feeble structure, have their wings modified (Cethosia, Limenitis, Junonia, Cynthia), while the large-bodied powerful species, which have all an excessively rapid flight, have exactly the same form of wing in Celebes as in the other islands. On the whole, therefore, we may say that all the butterflies of rather large size, conspicuous colours, and not very swift flight have been affected in the manner described, while the smaller sized and obscure groups, as well as those which are the objects of mimicry, and also those of exceedingly swift flight have remained unaffected.

It would thus appear as if there must be (or once have been) in the island of Celebes, some peculiar enemy to these larger-sized butterflies which does not exist, or is less abundant, in the surrounding islands. Increased powers of flight, or rapidity of turning, was advantageous in baffling this enemy; and the peculiar form of wing necessary to give this would be readily acquired by the action of "natural selection" on the slight variations of form that are continually occurring.

Such an enemy one would naturally suppose to be

an insectivorous bird ; but it is a remarkable fact that most of the genera of Fly-catchers of Borneo and Java on the one side (*Muscipeta*, *Philentoma*,) and of the Moluccas on the other (*Monarcha*, *Rhipidura*), are almost entirely absent from Celebes. Their place seems to be supplied by the Caterpillar-catchers (*Graucalus*, *Campephaga*, &c.), of which six or seven species are known from Celebes and are very numerous in individuals. We have no positive evidence that these birds pursue butterflies on the wing, but it is highly probable that they do so when other food is scarce. Mr. Bates has suggested to me that the larger Dragon-flies (*Æshna*, &c.) prey upon butterflies ; but I did not notice that they were more abundant in Celebes than elsewhere. However this may be, the fauna of Celebes is undoubtedly highly peculiar in every department of which we have any accurate knowledge ; and though we may not be able satisfactorily to trace how it has been effected, there can, I think, be little doubt that the singular modification in the wings of so many of the butterflies of that island is an effect of that complicated action and reaction of all living things upon each other in the struggle for existence, which continually tends to readjust disturbed relations, and to bring every species into harmony with the varying conditions of the surrounding universe.

But even the conjectural explanation now given fails us in the other cases of local modification. Why the species of the Western islands should be smaller than those further east,—why those of Amboyna should

exceed in size those of Gilolo and New Guinea—why the tailed species of India should begin to lose that appendage in the islands, and retain no trace of it on the borders of the Pacific,—and why, in three separate cases, the females of Amboyna species should be less gaily attired than the corresponding females of the surrounding islands,—are questions which we cannot at present attempt to answer. That they depend, however, on some general principle is certain, because analogous facts have been observed in other parts of the world. Mr. Bates informs me that, in three distinct groups, Papilios which on the Upper Amazon and in most other parts of South America have spotless upper wings obtain pale or white spots at Pará and on the Lower Amazon; and also that the *Æneas*-group of Papilios never have tails in the equatorial regions and the Amazons valley, but gradually acquire tails in many cases as they range towards the northern or southern tropic. Even in Europe we have somewhat similar facts; for the species and varieties of butterflies peculiar to the island of Sardinia are generally smaller and more deeply coloured than those of the mainland, and the same has recently been shown to be the case with the common tortoiseshell butterfly in the Isle of Man; while *Papilio Hospiton*, peculiar to the former island, has lost the tail, which is a prominent feature of the closely allied *P. Machaon*.

Facts of a similar nature to those now brought forward would no doubt be found to occur in other groups of insects, were local faunas carefully studied in

relation to those of the surrounding countries; and they seem to indicate that climate and other physical causes have, in some cases, a very powerful effect in modifying specific form and colour, and thus directly aid in producing the endless variety of nature.

Mimicry.

Having fully discussed this subject in the preceding essay, I have only to adduce such illustrations of it, as are furnished by the Eastern Papilionidæ, and to show their bearing upon the phenomena of variation already mentioned. As in America, so in the Old World, species of Danaidæ are the objects which the other families most often imitate. But besides these, some genera of Morphidæ and one section of the genus Papilio are also less frequently copied. Many species of Papilio mimic other species of these three groups so closely that they are undistinguishable when on the wing; and in every case the pairs which resemble each other inhabit the same locality.

The following list exhibits the most important and best marked cases of mimicry which occur among the Papilionidæ of the Malayan region and India :—

Mimickers.	Species mimicked.	Common habitat.
DANAIDÆ.		
1. Papilio paradoxa (male & female)	Euplœa Midamus (male & female)	} Sumatra, &c.
2. P. Caunus	E. Rhadamanthus.	
3. P. Thule	Danais sobrina ...	New Guinea.
4. P. Macareus	D. Aglaia	Malacca, Java.

Mimickers.	Species mimicked.	Common habitat.
DANAIDÆ.		
5. <i>Papilio</i> <i>Agestor</i> ...	<i>Danais</i> <i>Tytia</i>	Northern India.
6. <i>P.</i> <i>Idæoides</i> ...	<i>Hestia</i> <i>Leuconoë</i> ...	Philippines.
7. <i>P.</i> <i>Delessertii</i> ...	<i>Ideopsis</i> <i>daos</i> ...	Penang.
MORPHIDÆ.		
8. <i>P.</i> <i>Pandion</i> (female)... ..	<i>Drusilla</i> <i>bioculata</i> .	New Guinea.
PAPILIO (POLYDORUS- and COON-groups).		
9. <i>P.</i> <i>Pammon</i> (<i>Romulus</i> , female)...	<i>Papilio</i> <i>Hector</i> ...	India.
10. <i>P.</i> <i>Theseus</i> , var. (female)	<i>P.</i> <i>Antiphus</i>	Sumatra, Borneo.
11. <i>P.</i> <i>Theseus</i> , var. (female)	<i>P.</i> <i>Diphilus</i>	Sumatra, Java.
12. <i>P.</i> <i>Memnon</i> , var. (<i>Achates</i> , female)	<i>P.</i> <i>Coon</i>	Sumatra.
13. <i>P.</i> <i>Androgeus</i> , var. (<i>Achates</i> , female)	<i>P.</i> <i>Doubledayi</i> ...	Northern India.
14. <i>P.</i> <i>Ænomaus</i> (female)... ..	<i>P.</i> <i>Liris</i>	Timor.

We have, therefore, fourteen species or marked varieties of *Papilio*, which so closely resemble species of other groups in their respective localities, that it is not possible to impute the resemblance to accident. The first two in the list (*Papilio paradoxa* and *P. Caunus*) are so exactly like *Euplœa Midamus* and *E. Rhadamanthus* on the wing, that although they fly very slowly, I was quite unable to distinguish them. The first is a very interesting case, because the male and female differ considerably, and each mimics the corresponding sex of the *Euplœa*. A new species of *Papilio* which I discovered in New Guinea resembles *Danais sobrina*,

from the same country, just as *Papilio Marcareus* resembles *Danais Aglaia* in Malacca, and (according to Dr. Horsfield's figure) still more closely in Java. The Indian *Papilio Agestor* closely imitates *Danais Tytia*, which has quite a different style of colouring from the preceding; and the extraordinary *Papilio Idæoides* from the Philippine Islands, must, when on the wing, perfectly resemble the *Hestia Leuconoë* of the same region, as also does the *Papilio Delessertii* imitate the *Ideopsis daos* from Penang. Now in every one of these cases the *Papilios* are very scarce, while the *Danaidæ* which they resemble are exceedingly abundant—most of them swarming so as to be a positive nuisance to the collecting entomologist by continually hovering before him when he is in search of newer and more varied captures. Every garden, every roadside, the suburbs of every village are full of them, indicating very clearly that their life is an easy one, and that they are free from persecution by the foes which keep down the population of less favoured races. This superabundant population has been shown by Mr. Bates to be a general characteristic of all American groups and species which are objects of mimicry; and it is interesting to find his observations confirmed by examples on the other side of the globe.

The remarkable genus *Drusilla*, a group of pale-coloured butterflies, more or less adorned with ocellate spots, is also the object of mimicry by three distinct genera (*Melanitis*, *Hyantis*, and *Papilio*). These insects, like the *Danaidæ*, are abundant in individuals,

have a very weak and slow flight, and do not seek concealment, or appear to have any means of protection from insectivorous creatures. It is natural to conclude, therefore, that they have some hidden property which saves them from attack; and it is easy to see that when any other insects, by what we call accidental variation, come more or less remotely to resemble them, the latter will share to some extent in their immunity. An extraordinary dimorphic form of the female of *Papilio Ormenus* has come to resemble the *Drusillas* sufficiently to be taken for one of that group at a little distance; and it is curious that I captured one of these *Papilios* in the Aru Islands hovering along the ground, and settling on it occasionally, just as it is the habit of the *Drusillas* to do. The resemblance in this case is only general; but this form of *Papilio* varies much, and there is therefore material for natural selection to act upon, so as ultimately to produce a copy as exact as in the other cases.

The eastern *Papilios* allied to *Polydorus*, *Coon*, and *Philoxenus*, form a natural section of the genus resembling, in many respects, the *Æneas*-group of South America, which they may be said to represent in the East. Like them, they are forest insects, have a low and weak flight, and in their favourite localities are rather abundant in individuals; and like them, too, they are the objects of mimicry. We may conclude, therefore, that they possess some hidden means of protection, which makes it useful to other insects to be mistaken for them.

The Papilios which resemble them belong to a very distinct section of the genus, in which the sexes differ greatly; and it is those females only which differ most from the males, and which have already been alluded to as exhibiting instances of dimorphism, which resemble species of the other group.

The resemblance of *P. Romulus* to *P. Hector* is, in some specimens, very considerable, and has led to the two species being placed following each other in the British Museum Catalogues and by Mr. E. Doubleday. I have shown, however, that *P. Romulus* is probably a dimorphic form of the female *P. Pammon*, and belongs to a distinct section of the genus.

The next pair, *Papilio Theseus*, and *P. Antiphus*, have been united as one species both by De Haan and in the British Museum Catalogues. The ordinary variety of *P. Theseus* found in Java almost as nearly resembles *P. Diphilus*, inhabiting the same country. The most interesting case, however, is the extreme female form of *P. Memnon* (figured by Cramer under the name of *P. Achates*), which has acquired the general form and markings of *P. Coon*, an insect which differs from the ordinary male *P. Memnon*, as much as any two species which can be chosen in this extensive and highly varied genus; and, as if to show that this resemblance is not accidental, but is the result of law, when in India we find a species closely allied to *P. Coon*, but with red instead of yellow spots (*P. Doubledayi*), the corresponding variety of *P. Androgeus* (*P. Achates*, Cramer, 182,

A, B,) has acquired exactly the same peculiarity of having red spots instead of yellow. Lastly, in the island of Timor, the female of *P. CEnomaus* (a species allied to *P. Memnon*) resembles so closely *P. Liris* (one of the *Polydorus*-group), that the two, which were often seen flying together, could only be distinguished by a minute comparison after being captured.

The last six cases of mimicry are especially instructive, because they seem to indicate one of the processes by which dimorphic forms have been produced. When, as in these cases, one sex differs much from the other, and varies greatly itself, it may happen that occasionally individual variations will occur having a distant resemblance to groups which are the objects of mimicry, and which it is therefore advantageous to resemble. Such a variety will have a better chance of preservation; the individuals possessing it will be multiplied; and their accidental likeness to the favoured group will be rendered permanent by hereditary transmission, and, each successive variation which increases the resemblance being preserved, and all variations departing from the favoured type having less chance of preservation, there will in time result those singular cases of two or more isolated and fixed forms, bound together by that intimate relationship which constitutes them the sexes of a single species. The reason why the females are more subject to this kind of modification than the males is, probably, that their slower flight, when laden with eggs, and their exposure to attack while in the act of depositing their eggs

upon leaves, render it especially advantageous for them to have some additional protection. This they at once obtain by acquiring a resemblance to other species which, from whatever cause, enjoy a comparative immunity from persecution.

Concluding remarks on Variation in Lepidoptera.

This summary of the more interesting phenomena of variation presented by the eastern Papilionidæ is, I think, sufficient to substantiate my position, that the Lepidoptera are a group that offer especial facilities for such inquiries; and it will also show that they have undergone an amount of special adaptive modification rarely equalled among the more highly organized animals. And, among the Lepidoptera, the great and pre-eminently tropical families of Papilionidæ and Danaidæ seem to be those in which complicated adaptations to the surrounding organic and inorganic universe have been most completely developed, offering in this respect a striking analogy to the equally extraordinary, though totally different, adaptations which present themselves in the Orchideæ, the only family of plants in which mimicry of other organisms appears to play any important part, and the only one in which cases of conspicuous polymorphism occur; for as such we must class the male, female, and hermaphrodite forms of *Catasetum tridentatum*, which differ so greatly in form and structure that they were long considered to belong to three distinct genera.

*Arrangement and Geographical Distribution of the
Malayan Papilionidæ.*

Arrangement.—Although the species of Papilionidæ inhabiting the Malayan region are very numerous, they all belong to three out of the nine genera into which the family is divided. One of the remaining genera (*Eurycus*) is restricted to Australia, and another (*Teinopalpus*) to the Himalayan Mountains, while no less than four (*Parnassius*, *Doritis*, *Thais*, and *Sericius*) are confined to Southern Europe and to the mountain-ranges of the Palæarctic region.

The genera *Ornithoptera* and *Leptocircus* are highly characteristic of Malayan entomology, but are uniform in character and of small extent. The genus *Papilio*, on the other hand, presents a great variety of forms, and is so richly represented in the Malay Islands, that more than one-fourth of all the known species are found there. It becomes necessary, therefore, to divide this genus into natural groups before we can successfully study its geographical distribution.

Owing principally to Dr. Horsfield's observations in Java, we are acquainted with a considerable number of the larvæ of *Papilios*; and these furnish good characters for the primary division of the genus into natural groups. The manner in which the hinder wings are plaited or folded back at the abdominal margin, the size of the anal valves, the structure of the antennæ, and the form of the wings are also of much service, as well as the character of the flight and the style of

colouration. Using these characters, I divide the Malayan Papilios into four sections, and seventeen groups, as follows:—

Genus ORNITHOPTERA.

- | | | |
|----------------------|---|-------------------|
| a. Priamus-group. | } | Black and green. |
| c. Brookeanus-group. | | |
| b. Pompeus-group. | | Black and yellow. |

Genus PAPILIO.

A. Larvæ short, thick, with numerous fleshy tubercles; of a purplish colour.

- a. Nox-group. Abdominal fold in male very large; anal valves small, but swollen; antennæ moderate; wings entire, or tailed; includes the Indian *Philoxenus*-group.
- b. Coon-group. Abdominal fold in male small; anal valves small, but swollen; antennæ moderate; wings tailed.
- c. *Polydorus*-group. Abdominal fold in male small, or none; anal valves small or obsolete, hairy; wings tailed or entire.

B. Larvæ with third segment swollen, transversely or obliquely banded; pupa much bent. Imago with abdominal margin in male plaited, but not reflexed; body weak; antennæ long; wings much dilated, often tailed.

- d. *Ulysses*-group.
 - e. *Peranthus*-group.
 - f. *Memnon*-group.
- | | |
|---|--|
| { | Protenor-group (Indian) is somewhat intermediate between these, and is nearest to the Nox-group. |
|---|--|
- g. *Helenus*-group.
 - h. *Erectheus*-group.
 - i. *Pammon*-group.
 - k. *Demolion*-group.

C. Larvæ subcylindrical, variously coloured. Imago with abdominal margin in male plaited, but not reflexed; body weak; antennæ short, with a thick curved club; wings entire.

- l. Erithonius-group. Sexes alike, larva and pupa something like those of *P. Demolion*.
 - m. Paradoxa-group. Sexes different.
 - n. Dissimilis - group. Sexes alike; larva bright-coloured; pupa straight, cylindric.
- D. Larvæ elongate, attenuate behind, and often bifid, with lateral and oblique pale stripes, green. Imago with the abdominal margin in male reflexed, woolly or hairy within; anal valves small, hairy; antennæ short, stout; body stout.
- o. Macareus-group. Hind wings entire.
 - p. Antiphates-group. Hind wings much tailed (swallow-tails).
 - q. Eurypylus-group. Hind wings elongate or tailed.

Genus LEPTOCIRCUS.

Making, in all, twenty distinct groups of Malayan Papilionidæ.

The first section of the genus *Papilio* (A) comprises insects which, though differing considerably in structure, having much general resemblance. They all have a weak, low flight, frequent the most luxuriant forest-districts, seem to love the shade, and are the objects of mimicry by other *Papilios*.

Section B consists of weak-bodied, large-winged insects, with an irregular wavering flight, and which, when resting on foliage, often expand the wings, which the species of the other sections rarely or never do. They are the most conspicuous and striking of eastern Butterflies.

Section C consists of much weaker and slower-flying insects, often resembling in their flight, as well as in their colours, species of *Danaidæ*.

Section D contains the strongest-bodied and most swift-flying of the genus. They love sunlight, and frequent the borders of streams and the edges of puddles, where they gather together in swarms consisting of several species, greedily sucking up the moisture, and, when disturbed, circling round in the air, or flying high and with great strength and rapidity.

Geographical Distribution.—One hundred and thirty species of Malayan Papilionidæ are now known within the district extending from the Malay peninsula, on the north-west, to Woodlark Island, near New Guinea, on the south-east.

The exceeding richness of the Malayan region in these fine insects is seen by comparing the number of species found in the different tropical regions of the earth. From all Africa only 33 species of *Papilio* are known; but as several are still undescribed in collections, we may raise their number to about 40. In all tropical Asia there are at present described only 65 species, and I have seen in collections but two or three which have not yet been named. In South America, south of Panama, there are 150 species, or about one-seventh more than are yet known from the Malayan region; but the area of the two countries is very different; for while South America (even excluding Patagonia) contains 5,000,000 square miles, a line encircling the whole of the Malayan islands would only include an area of 2,700,000 square miles, of which the land-area would be about 1,000,000 square miles. This superior

richness is partly real and partly apparent. The breaking up of a district into small isolated portions, as in an archipelago, seems highly favourable to the segregation and perpetuation of local peculiarities in certain groups; so that a species which on a continent might have a wide range, and whose local forms, if any, would be so connected together that it would be impossible to separate them, may become by isolation reduced to a number of such clearly defined and constant forms that we are obliged to count them as species. From this point of view, therefore, the greater proportionate number of Malayan species may be considered as apparent only. Its true superiority is shown, on the other hand, by the possession of three genera and twenty groups of Papilionidæ against a single genus and eight groups in South America, and also by the much greater average size of the Malayan species. In most other families, however, the reverse is the case, the South American Nymphalidæ, Satyridæ, and Erycinidæ far surpassing those of the East in number, variety, and beauty.

The following list, exhibiting the range and distribution of each group, will enable us to study more easily their internal and external relations.

Range of the Groups of Malayan Papilionidæ.

Ornithoptera.

- | | | | |
|-----------------------|-----------------------------------|----|----------|
| 1. Priamus - group. | Moluccas to Woodlark | | |
| | Island | 5 | species. |
| 2. Pompeus - group. | Himalayas to New | | |
| | Guinea, (Celebes, maximum) | 11 | „ |
| 3. Brookeana - group. | Sumatra and Borneo .. | 1 | „ |

Papilio.

4. Nox-group.	North India, Java, and Philip-								
	pines	5	species.
5. Coon-group.	North India to Java...	...						2	„
6. Polydorus-group.	India to New Guinea								
	and Pacific	7	„
7. Ulysses-group.	Celebes to New Caledonia							4	„
8. Peranthus - group.	India to Timor and								
	Moluccas (India, maximum)	9	„
9. Memnon-group.	India to Timor and Mo-								
	luccas (Java, maximum)	10	„
10. Helenus-group.	Africa and India to New								
	Guinea	11	„
11. Pammon-group.	India to Pacific and Aus-								
	tralia	9	„
12. Erectheus-group.	Celebes to Australia ...							8	„
13. Demolion-group.	India to Celebes ...							2	„
14. Erithonius-group.	Africa, India, Australia							1	„
15. Paradoxa-group.	India to Java (Borneo,								
	maximum)	5	„
16. Dissimilis-group.	India to Timor (India,								
	maximum)	2	„
17. Macareus-group.	India to New Guinea ...							10	„
18. Antiphates-group.	Widely distributed ...							8	„
19. Eurypylus-group.	India to Australia ...							15	„

Leptocircus.

20 Leptocircus-group.	India to Celebes ...							4	„
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This Table shows the great affinity of the Malayan with the Indian Papilionidæ, only three out of the nineteen groups ranging beyond, into Africa, Europe, or America. The limitation of groups to the Indo-Malayan or Austro-Malayan divisions of the archipelago, which is so well marked in the higher animals, is much less conspicuous in insects, but is shown in some degree by the Papilionidæ. The following groups

are either almost or entirely restricted to one portion of the archipelago:—

Indo-Malayan Region.

Nox-group.
Coon-group.
Macareus-group (nearly).
Paradoxa-group.
Dissimilis-group (nearly).
Brookeanus-group.
LEPTOCIRCUS (genus).

Austro-Malayan Region.

Priamus-group.
Ulysses-group.
Erechtheus-group.

The remaining groups, which range over the whole archipelago, are, in many cases, insects of very powerful flight, or they frequent open places and the sea-beach, and are thus more likely to get blown from island to island. The fact that three such characteristic groups as those of Priamus, Ulysses, and Erechtheus are strictly limited to the Australian region of the archipelago, while five other groups are with equal strictness confined to the Indian region, is a strong corroboration of that division which has been founded almost entirely on the distribution of Mammalia and Birds.

If the various Malayan islands have undergone recent changes of level, and if any of them have been more closely united within the period of existing species than they are now, we may expect to find indications of such changes in community of species between islands now widely separated; while those islands which have long remained isolated would have had time to acquire peculiar forms by a slow and natural process of modification.

An examination of the relations of the species of the adjacent islands, will thus enable us to correct opinions formed from a mere consideration of their relative positions. For example, looking at a map of the archipelago, it is almost impossible to avoid the idea that Java and Sumatra have been recently united; their present proximity is so great, and they have such an obvious resemblance in their volcanic structure. Yet there can be little doubt that this opinion is erroneous, and that Sumatra has had a more recent and more intimate connexion with Borneo than it has had with Java. This is strikingly shown by the mammals of these islands—very few of the species of Java and Sumatra being identical, while a considerable number are common to Sumatra and Borneo. The birds show a somewhat similar relationship; and we shall find that the distribution of the Papilionidæ tells exactly the same tale. Thus:—

Sumatra has...	21 species	}	20 sp. common to both islands;
Borneo ,, ...	30 ,,		
Sumatra ,, ...	21 ,,	}	11 sp. common to both islands ;
Java ,, ...	28 ,,		
Borneo ,, ...	30 ,,	}	20 sp. common to both islands ;
Java ,, ...	28 ,,		

showing that both Sumatra and Java have a much closer relationship to Borneo than they have to each other—a most singular and interesting result, when we consider the wide separation of Borneo from them both, and its very different structure. The evidence furnished by a single group of insects would have had

but little weight on a point of such magnitude if standing alone; but coming as it does to confirm deductions drawn from whole classes of the higher animals, it must be admitted to have considerable value.

We may determine in a similar manner the relations of the different Papuan Islands to New Guinea. Of thirteen species of Papilionidæ obtained in the Aru Islands, six were also found in New Guinea, and seven not. Of nine species obtained at Waigiou, six were New Guinea, and three not. The five species found at Mysol were all New Guinea species. Mysol, therefore, has closer relations to New Guinea than the other islands; and this is corroborated by the distribution of the birds, of which I will only now give one instance. The Paradise Bird found in Mysol is the common New Guinea species, while the Aru Islands and Waigiou have each a species peculiar to themselves.

The large island of Borneo, which contains more species of Papilionidæ than any other in the archipelago, has nevertheless only three peculiar to itself; and it is quite possible, and even probable, that one of these may be found in Sumatra or Java. The last-named island has also three species peculiar to it; Sumatra has not one, and the peninsula of Malacca only two. The identity of species is even greater than in birds or in most other groups of insects, and points very strongly to a recent connexion of the whole with each other and the continent.

Remarkable Peculiarities of the Island of Celebes.

If we now pass to the next island (Celebes), separated from those last mentioned by a strait not wider than that which divides them from each other, we have a striking contrast; for with a total number of species less than either Borneo or Java, no fewer than eighteen are absolutely restricted to it. Further east, the large islands of Ceram and New Guinea have only three species peculiar to each, and Timor has five. We shall have to look, not to single islands, but to whole groups, in order to obtain an amount of individuality comparable with that of Celebes. For example, the extensive group comprising the large islands of Java, Borneo, and Sumatra, with the peninsula of Malacca, possessing altogether 48 species, has about 24, or just half, peculiar to it; the numerous group of the Philippines possess 22 species, of which 17 are peculiar; the seven chief islands of the Moluccas have 27, of which 12 are peculiar; and the whole of the Papuan Islands, with an equal number of species, have 17 peculiar. Comparable with the most isolated of these groups is Celebes, with its 24 species, of which the large proportion of 18 are peculiar. We see, therefore, that the opinion I have elsewhere expressed, of the high degree of isolation and the remarkable distinctive features of this interesting island, is fully borne out by the examination of this conspicuous family of insects. A single straggling island with a few small satellites, it is zoologically of equal

importance with extensive groups of islands many times as large as itself; and standing in the very centre of the archipelago, surrounded on every side with islets connecting it with the larger groups, and which seem to afford the greatest facilities for the migration and intercommunication of their respective productions, it yet stands out conspicuous with a character of its own in every department of nature, and presents peculiarities which are, I believe, without a parallel in any similar locality on the globe.

Briefly to summarize these peculiarities, Celebes possesses three genera of mammals (out of the very small number which inhabit it) which are of singular and isolated forms, viz., *Cynopithecus*, a tailless Ape allied to the Baboons; *Anoa*, a straight-horned Antelope of obscure affinities, but quite unlike anything else in the whole archipelago or in India: and *Babirusa*, an altogether abnormal wild Pig. With a rather limited bird population, Celebes has an immense preponderance of species confined to it, and has also six remarkable genera (*Meropogon*, *Ceycopsis*, *Streptocitta*, *Enodes*, *Scissirostrum*, and *Megacephalon*) entirely restricted to its narrow limits, as well as two others (*Prioniturus* and *Basilornis*) which only range to a single island beyond it.

Mr. Smith's elaborate tables of the distribution of Malayan Hymenoptera (see "Proc. Linn. Soc." Zool. vol. vii.) show that out of the large number of 301 species collected in Celebes, 190 (or nearly two-thirds) are absolutely restricted to it, although Borneo on one

side, and the various islands of the Moluccas on the other, were equally well explored by me; and no less than twelve of the genera are not found in any other island of the archipelago. I have shown in the present essay that, in the Papilionidæ, it has far more species of its own than any other island, and a greater proportion of peculiar species than many of the large groups of islands in the archipelago—and that it gives to a large number of the species and varieties which inhabit it, 1st, an increase of size, and, 2nd, a peculiar modification in the form of the wings, which stamp upon the most dissimilar insects a mark distinctive of their common birth-place.

What, I would ask, are we to do with phenomena such as these? Are we to rest content with that very simple, but at the same time very unsatisfying explanation, that all these insects and other animals were created exactly *as* they are, and originally placed exactly *where* they are, by the inscrutable will of their Creator, and that we have nothing to do but to register the facts and wonder? Was this single island selected for a fantastic display of creative power, merely to excite a childlike and unreasoning admiration? Is all this appearance of gradual modification by the action of natural causes—a modification the successive steps of which we can almost trace—all delusive? Is this harmony between the most diverse groups, all presenting analogous phenomena, and indicating a dependence upon physical changes of which we have independent evidence, all false testimony? If I could think so, the