

**ALFRED
RUSSEL
WALLACE**

CONTRIBUTIONS TO THE
THEORY OF NATURAL
SELECTION

Alfred Wallace
Contributions to the
Theory of Natural Selection

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Contributions to the Theory of Natural Selection / A Series of Essays:*

Содержание

PREFACE	5
PREFACE TO THE SECOND EDITION	15
I.	16
Geographical Distribution dependent on Geologic Changes	16
A Law deduced from well-known Geographical and Geological Facts	20
The Form of a true system of Classification determined by this Law	23
Geographical Distribution of Organisms	26
Geological Distribution of the Forms of Life	31
High Organization of very ancient Animals consistent with this Law	33
Objections to Forbes' Theory of Polarity	36
Rudimentary Organs	42
Conclusion	44
II.	45
Instability of Varieties supposed to prove the permanent distinctness of Species	45
The Struggle for Existence	48
The Law of Population of Species	49
The Abundance or Rarity of a Species dependent upon its more or less perfect Adaptation to the	54

Conditions of Existence	
Useful Variations will tend to Increase; useless or hurtful Variations to Diminish	56
Superior Varieties will ultimately Extirpate the original Species	58
The Partial Reversion of Domesticated Varieties explained	60
Lamarck's Hypothesis very different from that now advanced	63
Conclusion	66
III.	67
Importance of the Principle of Utility	70
Popular Theories of Colour in Animals	71
Importance of Concealment as Influencing Colour	73
Special Modifications of Colour	77
Theory of Protective Colouring	90
Objection that Colour, as being dangerous, should not exist in Nature	94
Mimicry	100
Mimicry among Lepidoptera	103
Lepidoptera mimicking other Insects	116
Mimicry among Beetles	118
Конец ознакомительного фрагмента.	121

Alfred Russel Wallace

Contributions to the Theory of Natural Selection / A Series of Essays

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 publication 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.

III.—*Mimicry, and other Protective Resemblances among Animals.*

PAGE	
53	Additional illustration of protective colouring in the case of the wood-dove and the robin.
63	On moths resembling bird's dung and mortar.
86	Correction of some names of African Papilios and a reference to Mr. Trimen's observations.
89	Mr. Jenner Weir's observation on birds which refused to eat <i>Spilosoma menthrasti</i> .
102	An additional case of snake mimicry in <i>Oxyrhopus trigeminus</i> .
107	Mr. Savin's case of mimicry among hawks.
113	Name, <i>Diadema anomala</i> , added.
117 to 122.	Use of gay colours in caterpillars, with an account of Mr. Jenner Weir's and Mr. Butler's observations.

IV.—*The Malayan Papilionidæ or Swallow-tailed Butterflies, as illustrative of the Theory of Natural Selection.*

135 to 140.	Additions to the discussion on the rank of the Papilionidæ, and on the principles which determine the comparative rank of groups in the animal kingdom.
164	Illustration of variability from Mr. Baker's revision of the British Roses.
173	Additional facts, on local variations of colour.
196	Additional genus of birds (Ceycopsis) peculiar to Celebes.
199, 200.	Concluding remarks.

VI.—*The Philosophy of Birds' Nests.*

218	On nesting of Terns and Gulls, rewritten.
220 to 222.	Daines Barrington, and others, on the song of birds.
223	On young birds learning to build, by memory and imitation.
224	Levaillant, on mode of nest-building.
229	On imperfect adaptation in birds' nests.

VII.—*A Theory of Birds' Nests.*

231, 232.	Introductory passages modified, with some omissions.
233	How modifications of organization would affect the form of the nest.
235	Illustration from the habits of children and savages.
235, 236.	Objection to term "hereditary habit" answered.
237	Passage rewritten, on more or less variable characters in relation to nidification.
248	On males choosing or rejecting females, and on the various modes in which colour may be acquired by female birds.
249	On probable ancestral colours of female birds.
255	Protective colouring of the Waxwing.

VIII.—*Creation by Law.*

293	Amount of variation in dogs.
296, 297.	The "Times" on Natural Selection.
298 to 300.	On intermediate or generalized forms of extinct animals as an indication of transmutation or development.
302	Tabular demonstration of the Origin of Species by Natural Selection.

IX.—*The development of Human Races, under the law of Natural Selection.*

316	On colour as perhaps correlated with immunity from disease in man.
326, 327.	On the probable future development of man.
330	Concluding paragraph rewritten.

London, March, 1870.

PREFACE TO THE SECOND EDITION

The flattering reception of my Essays by the public and the press having led to a second edition being called for within a year of its first publication, I have taken the opportunity to make a few necessary corrections. I have also added a few passages to the 6th and 7th Essays, and have given two notes, explanatory of some portions of the last chapter which appear to have been not always understood. These additions are as follows:—

<i>To avoid altering the paging the additional pages now given have been lettered.</i>		
1st Ed.	2nd Ed.	
221	221	Additional facts as to birds acquiring the song of other species.
223	223A) 223B)	Mr. Spruce's remarks on young birds pairing with old.
228	228A) 228B)	Pouchet's observations on a change in the nests of swallows.
229	—	Passage omitted about nest of Golden Crested Warbler, which had been inserted on Rennie's authority, but has not been confirmed by any later observers.
261	261	Daines Barrington, on importance of protection to the female bird.
	372	Note A.
	372B	Note B.

I. ON THE LAW WHICH HAS REGULATED THE INTRODUCTION OF NEW SPECIES. ¹

Geographical Distribution dependent on Geologic Changes

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.

¹ Written at Sarawak in February, 1855, and published in the "Annals and Magazine of Natural History," September, 1855.

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 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 recent 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 phenomena of representative groups, and those which Professor Forbes supposed to manifest polarity. 4th. The phenomena

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 these systems of classification which arrange species or groups in circles, as well as these 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 Euploæas 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 phenomena as are exhibited by the Galapagos 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 phenomena, 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 phenomena 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.² We thus have a clue to the increase of the forms of life during certain periods, and their decrease during others, without recourse 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

² 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.

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 exuviae 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 objections 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 oeconomy, 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.³ Many more of these modifications should we behold, and more complete series 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.

³ 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 disuse, as explained by Mr. Darwin.

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. ⁴

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

⁴ Written at Ternate, February, 1858; and published in the Journal of the Proceedings of the Linnæan Society for August, 1858.

varieties occurring among wild animals, this argument has had great weight with naturalists, and has led to a very general and somewhat 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!⁵ 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 increase 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

⁵ This is under estimated. The number would really amount to more than two thousand millions!

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 remain 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*.⁶

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 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.

⁶ 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.

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 its 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 phenomena 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 phenomena 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 textbooks 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 phenomena, 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 phenomena, 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 earth-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, brush-wood, 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 scorpio*) 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 acesa*) 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 striae 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. *Agriopis 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 physical 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 concealed. 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 those 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 resemblance 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 anthedon*; 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 *Euplœa 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 *Euplœa 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 scorio* 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, *Pæciloderma 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.

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